JUVENILE BRISTOL BAY SOCKEYE SALMON ECOLOGY

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A

DISSERTATION

Presented to the Faculty

of the University of Alaska Fairbanks

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for the Degree of

DOCTOR OF PHILOSOPHY

By

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Abstract

Predicting annual returns of Bristol Bay sockeye salmon (*Oncorhynchus nerka*) has been difficult due to large, unexplained variations in return strength. Ocean conditions, particularly during the first few months after salmon leave freshwater, are believed to have a strong influence on their early marine growth and survival. Limited historical and present research suggests that sea temperature can affect juvenile Bristol Bay distribution. During years with cool spring sea temperatures, juvenile sockeye salmon are distributed nearshore along the Alaska Peninsula, whereas they are found further offshore during years with warm spring sea temperatures. Juvenile sockeye salmon are larger, in better condition, and have higher marine stage survival after the first year at sea when they are distributed further offshore than when they are distributed nearshore along the Alaska Peninsula. Juvenile sockeye salmon stomach contents also shift from primarily Pacific sand lance (*Ammodytes hexapterus*) and euphausiids to age 0 walleye pollock (*Theragra chalcogramma*) when their distribution changes from nearshore to further offshore. Annual averages of juvenile sockeye salmon growth rate potential (GRP) were generally lower among years and regions with cool spring sea temperatures. In addition, juvenile sockeye salmon GRP was generally higher in offshore regions than nearshore regions of the eastern Bering Sea shelf. A sensitivity analysis indicated that juvenile sockeye salmon GRP was more sensitive to changes in observed (August to September) sea surface temperatures during years when prey densities were lower. The results of the dissertation suggest that variability in early marine survival is

primarily due to bottom-up control of the trophic structure of the eastern Bering Sea ecosystem.

Table of Contents

Page

Page

Page

List of Figures

Page

Page

List of Tables

Page

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The study on Bristol Bay sockeye salmon ecology was made possible with the help of a number of people inside and outside of the Federal Government.

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General Introduction

Unanticipated changes in productivity of Pacific salmon (*Oncorhynchus* spp) from major western Alaska rivers and lake systems draining to the Bering Sea are affecting western Alaska communities through declines in harvest for subsistence and commercial fisheries. For instance, commercial harvest of Chinook (*O. tshawytscha*) and chum (*O. keta*) salmon to the Yukon, Kuskokwim, and Norton Sound (AYK) regions during 1997 and 1998 were less than 50 percent of the available 30 to 40-year average (Kruse 1998). Returns of sockeye (*O. nerka*) salmon to the Bristol Bay region during 1997 and 1998 were near 50% of the expected returns for those years (Kruse 1998). Returns of adult salmon to western Alaska remained low during 2001 and 2002; however, recent (2003 to 2006) returns have been large in comparison to previous years (see http://www.cf.adfg.ak.us for details), highlighting the need to understand why wild swings in annual run strength in salmon returns to western Alaska occur.

The causes of variation in adult salmon run strength are not fully understood, but may be related to changes in the marine environment. Fishery scientists generally agree that conditions in the ocean, particularly in the first few months after salmon leave freshwater, strongly influence salmon survival (Holtby et al. 1990; Friedland et al. 1996; Beamish and Mahnken 2001). The assumption is that the growth rate of juvenile salmon in the estuarine and nearshore marine environments is directly linked to their marine survival. Thus, years with favorable environmental conditions and increased growth rates of juvenile salmon may result in reducing their susceptibility to size-selective predation (Fisher and Pearcy 1988; Holtby et al. 1990; Friedland et al. 2000) and/or

improving survival during their first winter at sea (Beamish and Mahnken 2001), ultimately affecting total returns of salmon in the following years.

In this dissertation, I examine the linkages between early marine growth rates, environment, and marine survival of salmon of Bristol Bay sockeye salmon. In Chapter 1, I present historical information on juvenile salmon research in the eastern Bering Sea. Research during the late 1960s to early 1970s and mid 1980s indicated that the distribution and migration pathways of juvenile sockeye salmon were southwest along the Alaska Peninsula from nearshore to 110 km offshore, whereas research conducted during 2000 to 2006 indicated that their distribution and migration could also be farther offshore. Research presented in this dissertation indicates that sea temperatures, particularly during spring and summer, affect juvenile sockeye salmon distribution. Evidence that the offshore migratory pathway of juvenile sockeye salmon can be associated with larger sized fish, higher condition indices, marine survival, and relative abundance is presented. Bottom-up control of the ecosystem is the most plausible mechanism regulating the size of juvenile sockeye salmon, by which warm spring sea temperatures are associated with increased productivity on the eastern Bering Sea shelf.

In Chapter 2, I present evidence that larger juvenile sockeye salmon have higher marine survival using size data from archived scales from returning adult sockeye salmon and trawl samples of juvenile sockeye salmon collected along the eastern Bering Sea shelf during 2000 to 2002. The size of juvenile sockeye salmon correlated with indices of their marine survival rate (i.e., smaller fish had lower indices of marine survival rate). However, there was no relationship between the size of sockeye salmon after their first

year at sea as estimated from archived scales and brood-year survival; size was relatively uniform over the time-series, possibly indicating size-selective mortality on smaller individuals during marine residence. Variation in size, relative abundance, and marine survival rate of juvenile sockeye salmon is likely related to ocean conditions affecting their early marine migratory pathways along the eastern Bering Sea shelf.

In Chapter 3, interannual variations in distribution, size, indices of feeding and condition of juvenile Bristol Bay sockeye salmon collected in August – September (2000 – 2003) during Bering – Aleutian Salmon International Surveys are examined to test possible mechanisms influencing their early marine growth and survival. Juvenile sockeye salmon were mainly distributed within the southern region of the eastern Bering Sea, south of 57° N during 2000 and 2001 and farther offshore, south of 58° N during 2002 and 2003. In general, juvenile sockeye salmon were significantly larger ($P < 0.05$) and had significantly higher indices of condition ($P < 0.05$) during 2002 and 2003 than during 2000 and 2001. The feeding index was generally higher for age 1.0 sockeye salmon than age 2.0 during all years. Among-year comparisons suggested that Pacific sand lance (*Ammodytes hexapterus*) were important components of the juvenile sockeye salmon diet during 2000 and 2001 (20% to 50% of the mean wet mass) and age 0 pollock (*Theragra chalcogramma*) were important components during 2002 and 2003 (50% to 60% of the mean wet mass). Warmer sea temperatures during spring and summer of 2002 and 2003 likely increased copepod productivity on the eastern Bering Sea shelf, enhancing juvenile sockeye salmon growth.

In Chapter 4, a spatially explicit bioenergetics model is used to predict juvenile sockeye salmon growth rate potential (GRP) along the eastern Bering Sea shelf during years with cool and warm spring sea temperatures. Annual averages of juvenile sockeye salmon GRP were generally lower among years and regions with cool spring SSTs. In addition, juvenile sockeye salmon growth rate potential was generally higher in offshore than nearshore regions of the eastern Bering Sea shelf. The size and distribution (catch per unit effort) of juvenile sockeye salmon were not significantly ($P > 0.05$) related to GRP; this result was likely due to stock-specific dynamics (freshwater age structure) and annual variability in early marine growth prior to the August – September survey. Juvenile sockeye salmon prey densities were positively related to spring SST ($P < 0.05$). A sensitivity analysis indicated that juvenile sockeye salmon GRP was more sensitive to changes in observed SST during years when prey densities were lower (2000 – 2002, and 2006). These results suggest the importance of bottom-up control on the eastern Bering Sea ecosystem for habitat quality of juvenile sockeye salmon in this region.

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1 RESEARCH ON JUVENILE BRISTOL BAY SOCKEYE SALMON IN THE EASTERN BERING SEA: A HISTORICAL PERSPECTIVE[1]

1.1 Abstract

Research on juvenile Bristol Bay sockeye salmon from the mid 1960s to present is summarized. Research during the late 1960s to early 1970s and mid 1980s indicated that the distribution and migration pathways of juvenile sockeye salmon were along the Alaska Peninsula from nearshore to 110 km offshore, whereas research conducted during 2000 to 2006 indicated that their distribution and migration extends further offshore. Results suggest that sea temperatures, particularly during spring and summer, affect juvenile sockeye salmon distribution. Evidence that the offshore migratory pathway of juvenile sockeye salmon is associated with larger sized fish, higher condition indices, marine survival, and relative abundance is presented. Bottom-up control of the ecosystem was the most plausible mechanism regulating the size of juvenile sockeye salmon, where warm spring sea temperatures are associated with increased productivity on the eastern Bering Sea shelf.

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[1] Farley, E. V., Jr. In Review. Research on juvenile Bristol Bay sockeye salmon in the eastern Bering Sea: a historical perspective. Marine Fisheries Review.

1.2 Introduction

Sockeye salmon (*Oncorhynchus nerka*) returns to Bristol Bay are the largest in the world. Annual returns of adult sockeye salmon to the region have varied widely over the past 48 years, ranging from a low 5 million to approximately 75 million (Figure 1.1). Peak returns generally occurred every 5 years prior to the mid 1970s mostly due to cyclic returns of adult sockeye salmon to the Kvichak River system (Eggers and Rogers, 1987). The large variability in the number of returning adult sockeye salmon poses problems for the fishing industry when trying to prepare for harvest, processing, transportation, and sale of sockeye salmon. Even though the variability in returns has been attributed to annual and decadal fluctuations in climate and ocean environment (Rogers 1984; Hare and Francis, 1995; Adkison et al., 1996; Downton and Miller, 1998; Peterman et al., 1998; Mueter et al., 2002), incorporating climate data into forecast models of Bristol Bay returns has not improved forecast accuracy (Adkison and Peterman, 1999).

Bristol Bay sockeye salmon survival is influenced by regional-scale processes (Peterman et al., 1998), in particular summer sea surface temperatures in the eastern Bering Sea during the juvenile life history stage (Mueter et al., 2002). Fishery scientists generally agree that conditions in the ocean, particularly in the first few months after leaving freshwater, strongly influence interannual variability in salmon survival and growth (Parker, 1962; Pearcy, 1992). Sea temperature can regulate production of potential salmon prey (i.e., zooplankton; Corkett and McLaren, 1978; Huntly and Lopez, 1992; Hunt and Stabeno, 2002) and can affect salmon consumption and growth rates of salmon (Donaldson and Foster, 1940). Correlation analyses (i.e., Mueter et al., 2002)

provide possible links to climate and salmon marine survival, yet describing how the climate variable influences marine survival is speculative at best, as basic information on the early marine life history of salmon is generally lacking, especially for western Alaska salmon stocks.

This paper summarizes historical (Ogi, 1973; Straty, 1974; Hartt and Dell, 1986; Isakson et al., 1986) and current (Farley et al., 2005) research on juvenile Bristol Bay sockeye salmon along the eastern Bering Sea shelf. A brief discussion of the marine life history characteristics of Bristol Bay sockeye salmon is followed by details on historical and current juvenile sockeye salmon research conducted along the eastern Bering Sea shelf. Results from the juvenile sockeye salmon research are discussed in relation to the leading hypothesis for ocean productivity on the eastern Bering Sea shelf (Hunt and Stabeno, 2002) that may be governing growth and survival of juvenile Bristol Bay sockeye salmon.

1.3 Marine life history of Bristol Bay sockeye salmon

Bristol Bay sockeye salmon generally spend two to three years in freshwater, migrate to sea, spend two to three years rearing in the ocean, and primarily return as 4-, 5-, and 6-year-old fish. Bristol Bay sockeye salmon smolt leave freshwater lakes during late May, shortly after the ice breaks up on the lakes, and the smolt outmigration can last into late June and beyond, depending on the number of lake systems the fish must pass through to get to the ocean (Burgner, 1991). Once juvenile sockeye salmon enter the marine environment of Bristol Bay they stay nearshore for feeding and growing (Straty and Jaenicke, 1980). After their first summer at sea, sockeye salmon tend to follow an

elliptical migration path that extends westerly toward the Kamchatka Peninsula then easterly to the Gulf of Alaska (Straty, 1975). Adult sockeye salmon return to Bristol Bay during late June through July. The onshore movement toward Bristol Bay begins during May with stocks of sockeye salmon migrating from the North Pacific Ocean into the eastern Bering Sea through Aleutian passes. Once in the eastern Bering Sea, the sockeye salmon move north for a considerable distance before moving east into Bristol Bay (Straty, 1975). Spawning generally begins in late July and can occur through October (Burgner, 1991).

1.4 Juvenile Bristol Bay sockeye salmon research along the eastern Bering Sea shelf.

1.4.1 *Fisheries Research Institute (1964 to 1968)*

Some of the earliest research on juvenile salmon along the eastern Bering Sea was conducted by the Fisheries Research Institute during 1964 to 1968 (Hartt and Dell, 1986). The survey area was the eastern Bering Sea shelf (Figure 1.2). The main objectives of the research were to determine the distribution and migration of juvenile salmon during their first summer at sea and to tag fish to determine major stocks in areas of high concentration. Secondary objectives were to study their feeding and growth and relationships to other marine fish species. The gear they used to sample juvenile salmon was a purse seine that was about 704 m long by 46 m deep. The mesh size in the seine was 63 mm in the lower half of the net and 51 mm in the upper half. The bunt section of the seine was 37 m long and was composed of 25 mm mesh. The seine was set in a semicircle and held open in the fishing position for 30 minutes. In addition, the purse

seine was fished in a manner that provided information on directional movement of fish by controlling the direction of the opening of the seine while it was held in fishing position.

Their results indicated that juvenile sockeye salmon in the eastern Bering Sea were primarily distributed between nearshore locations along the Alaska Peninsula to approximately 110 km offshore. The direction of migration inferred from directional setting of the purse seine indicated that the movement of juvenile sockeye salmon was apparently not directed specifically toward offshore migration, but instead the fish appeared to be lingering in the area surveyed. The predominant prey for juvenile sockeye salmon were euphausiids and larval fish, and these prey items were frequently observed from the vessel during purse seine operations when concentrations of juvenile salmon were present. Hartt and Dell (1986) speculated that the speed at which juvenile sockeye salmon migrate offshore could have been affected by areas of large prey concentrations, where they presumably slow their seaward migration rate in order to feed on large schools of prey.

Six tagged Bristol Bay juvenile sockeye salmon were recovered as adults 2 and 3 years later. The tagged fish provided stock origin at time of capture as juveniles. Comparisons between size as smolt leaving freshwater lakes and the size of these tagged individuals indicated that early marine growth rates for Nushagak, Naknek-Kvichak, and Egegik sockeye salmon ($n = 6$) were between 0.07 cm and 0.08 cm per day and that their early marine migration rate (river mouth to capture location offshore) was approximately 5.2 km per day (Hartt and Dell, 1986).

1.4.2 *US Fish and Wildlife Service (1965 to 1972)*

Early estuarine research by the Fish and Wildlife Service, Auke Bay Laboratory began during 1965 with the goal of providing basic information on the life history of sockeye salmon, during its seaward migration through Bristol Bay (Straty, 1974; Straty and Jaenicke, 1980). The survey area was within Bristol Bay, but also extended onto the eastern Bering Sea shelf (Figure 1.3). The goal of the research was to understand the relationship between critical environmental factors and the well-being of juvenile salmon during this period so that environmental influence upon stocks of Bristol Bay sockeye salmon in a given year might ultimately be predicted. Several gear types were experimented with to capture juvenile salmon including circular tow nets 2.1 m in diameter, a 185 m small-mesh lampara seine, a 110 m small-mesh round haul seine, variable-mesh monofilament nylon gill nets (55 mm, 42 mm, and 30 mm stretch measure), and a 365 m small-mesh purse seine. The 365 m purse seine proved to be the most effective gear for capturing young salmon and was the gear used in the studies for juvenile salmon research.

The major objective, to produce better predictions of Bristol Bay adult returns was never specifically addressed; nevertheless, several important insights into the early marine ecology of juvenile Bristol Bay sockeye salmon were found and summarized in Straty (1974) and Straty and Jaenicke (1980). One of the major findings of the research was that the seaward migration route of major stocks of Bristol Bay sockeye salmon was from the river mouths of major sockeye salmon producing rivers and along the coast of the Alaska Peninsula as far as Port Moller and perhaps Unimak Pass. Juvenile sockeye

salmon were believed to follow increasing salinity gradients as a means of marking their migration route. Sea temperature was also believed to influence distribution, and juvenile sockeye salmon were believed to distribute themselves in warmer nearshore waters of the eastern Bering Sea as opposed to the cooler offshore waters. The diets of juvenile sockeye salmon were composed mostly of Pacific sand lance (*Ammodytes hexapterus*), euphausiids, and copepods and juvenile sockeye salmon tended to have more food in their stomachs in the outer bay than closer to their natal rivers. Predation on juvenile sockeye salmon by other fish species seemed to be low. Straty and Jaenicke (1980) speculated that higher sea temperatures in Bristol Bay would likely result in more rapid growth and faster rate of seaward migration of juvenile sockeye salmon and that the faster growth rates would lead to higher marine survival of juvenile sockeye salmon.

1.4.3 *Hokkaido University (1969 to 1970)*

Research on juvenile Bristol Bay sockeye salmon offshore of Port Moller was also conducted by Hokkaido University during the summer months (late June to early August) of 1969 and 1970 (Ogi, 1973). The goal of the research was to clarify the ecology of Bristol Bay sockeye salmon during their early marine life history stage. The research was conducted in coordination with the US Fish and Wildlife Service sampling during the same years, and summaries of this research included fish samples from stations sampled by both parties.

The stations sampled by the R/V *Oshoro maru* are shown in Figure 1.4. A variable-mesh gillnet was used to sample fish at each station. The gillnet was allowed to fish for an average 9 hours during the day and 10 hours during night. Results suggested a

similar offshore distribution and migration pattern for juvenile sockeye salmon to that found by Straty (1974). In addition, freshwater age 2.0 (age was designated by the European notation, i.e., *a.b*, where *a* = the number of winters spent in freshwater prior to going to sea and *b* = the number of winters spent in the ocean; Koo, 1962) sockeye salmon were the predominant percent age group early on during the offshore migration, followed by freshwater age 1.0.

1.4.4 *Outer Continental Shelf Environmental Assessment Program (1984 to 1985)*

During late June to mid September 1984 and mid June to late July 1985, researchers from Dames & Moore and the Fisheries Research Institute (University of Washington) conducted surveys along the eastern Bering Sea shelf during summer and fall to provide baseline descriptions of fish assemblages to assess potential impacts of oil and gas development (Isakson et al., 1986). The primary objectives were to describe the demersal and pelagic species assemblages, determine relative abundance of these fish, and describe the temporal and spatial changes in distribution of fish. The research was conducted along transects offshore of the Alaska Peninsula from Ugashik Bay to southwest of Izembek Lagoon (Figure 1.5). Fish were sampled using a number of gear types, but the primary gear was a beach seine, purse seine, and a small purse seine.

Their results on offshore distribution and migration corridors largely confirmed the results found by Straty (1974) in that the migratory corridor for juvenile sockeye salmon between Ugashik and Port Heiden was less than about 28 km wide, whereas the migratory corridor was further offshore between Port Heiden and Izembek Lagoon. However, the hypothesis that juvenile sockeye salmon progressively move offshore with

increasing size was not strongly supported by their data. These results were likely influenced by the survey design, because the sampled transects did not extend as far offshore as those sampled during previous surveys.

Sockeye salmon smolt marking experiments performed by Straty (1974) during 1967 to 1970 were summarized in Isakson et al. (1986). The mean migration rate estimated for pooled stocks by year and for pooled years by stock indicate a grand mean of approximately 9.6 km/day, which they report is very close to 1 body length per second for juvenile Bristol Bay sockeye salmon of average length. The authors emphasized the pressing need for research to define the roles and consequences of biotic and abiotic variables in modifying salmon migrations.

1.4.5 *Ocean Carrying Capacity Program (2000 to 2006)*

Beginning in 2000, scientists from the National Marine Fisheries Service conducted research along the eastern Bering Sea shelf with a goal of determining mechanisms affecting marine survival of western Alaska juvenile salmon. The research named Bering-Aleutian Salmon International Survey (BASIS) was conducted in collaboration with member nations of the North Pacific Anadromous Fish Commission (NPAFC[2]). The portion of the surveys that focused on juvenile Bristol Bay sockeye salmon occurred during mid August to early September and sampled stations within Bristol Bay and offshore along the eastern Bering Sea shelf (Figure 1.6). Juvenile sockeye salmon were collected using a mid-water rope trawl that was rigged to fish the top 15 m of the water column (see Farley et al., 2005 for details). The mid-water rope

[2] North Pacific Anadromous Fish Commission. 2001. Plan for NPAFC Bering-Aleutian Salmon International Survey (BASIS) 2002 – 2006. NPAFC Doc. 579, Rev. 2. 27 p.

trawl was 198 m long, had hexagonal mesh in wings and body, and had a 1.2-cm mesh liner in the codend. The rope trawl was towed at 3.5 to 5 knots, and had a typical spread of 50 m horizontally and 12 m vertically.

Results indicated two different migration pathways for juvenile Bristol Bay sockeye salmon. The first migration pathway was west in an area defined from the Alaska Peninsula and extending offshore to 57°N, while the second migration pathway was farther offshore along the northern and southern sides of Bristol Bay (Farley et al., 2005; Farley et al., 2007c). Juvenile sockeye salmon indices of size, marine survival, gut content, condition, and growth rate potential in relation to nearshore versus offshore migration pathways are summarized in Table 1.1. In general, these recent studies indicated that fish were large, had higher marine-stage survival rates, and were in better condition when their migration pathway was farther offshore. In addition, growth rate potential in the offshore regions was higher than nearshore regions suggesting that juvenile sockeye salmon that distribute and migrate farther offshore would find themselves in areas of higher growth rate potential. Size selective mortality, particularly on smaller juvenile sockeye salmon, appears to be an important factor impacting their early marine survival (Farley et al., 2007b; Farley et al., 2007c).

1.5 Discussion

The first step toward understanding mechanisms associated with highly variable catch and brood return data for Bristol Bay sockeye salmon is to provide basic biological information during their most critical life history stages. This review examines the past

and present research on the ecology of juvenile Bristol Bay sockeye salmon. Can these results provide insight into ecological processes that affect marine survival of juvenile Bristol Bay sockeye salmon during this critical life history stage? First, the differences in the seaward migration pathways of Bristol Bay juvenile sockeye salmon (nearshore versus offshore) are likely related to sea-surface temperature along the eastern Bering Sea shelf. Juvenile sockeye salmon tend to seek or aggregate in warmer sea-surface temperatures to promote optimal migration, growth, and marine survival rates (Straty, 1974). Mid June to early July sea-surface temperatures, particularly offshore within Bristol Bay were cool during 1967 – 1971 (see Straty, 1974 for examples). Spring (and likely summer) sea temperatures were anomalously cool during 1984 and 1985 (Figure 1.7; i.e., OCSEAP study period) and spring and summer sea temperatures were also cool during 2000, 2001 and 2006 when compared to 2002 to 2005 (Figure 1.8; i.e., AFSC study period).

The years with cool sea temperatures along the eastern Bering Sea shelf were associated with nearshore distribution of juvenile Bristol Bay sockeye salmon. It is likely that juvenile sockeye salmon avoided the cooler waters offshore and instead distributed themselves in the relatively warmer surface waters found nearshore along the Alaska Peninsula (Straty, 1974). In contrast, the extensive offshore distribution of juvenile sockeye salmon during 2002 to 2005 may be the result of warmer offshore sea-surface temperatures during spring and summer (Farley et al., 2005; Farley et al., 2007b), where warmer sea temperatures offer opportunities for rapid offshore movement possibly due in

part to higher growth rates related to increased productivity on the eastern Bering Sea shelf (Farley et al., 2007c).

Second, years with warm sea temperatures are associated with higher productivity on the eastern Bering Sea shelf. Recently, a new oscillating control hypothesis (OCH) was proposed that provides a conceptual framework for understanding decadal-scale changes in climate and its importance to trophic structure on the eastern Bering Sea shelf (Hunt and Stabeno, 2002). The OCH predicts that during cold regimes, zooplankton prey for larval fish would be limited, negatively impacting recruitment of fish populations on the shelf. In contrast, warm regimes are associated with strong zooplankton productivity and higher survival of larval and juvenile fish. A warm regime was the most plausible explanation for juvenile sockeye salmon that were larger and in better condition when compared to fish collected during years with cool spring temperatures (Farley et al., 2007b). In support of this hypothesis, warm summer sea temperatures were also positively correlated with higher marine survival of western Alaska sockeye salmon (Mueter et al., 2002), whereas the cool sea temperatures during the early 1970s (Straty, 1974) appear to align with poor productivity of Bristol Bay sockeye salmon during the mid 1970s (Adkison et al., 1996).

In summary, early marine research on juvenile sockeye salmon has provided much needed information on this important life history stage for salmon. It is now known that the size of the fish after their first summer at sea is important to subsequent marine survival (Beamish and Mahnken, 2001; Beamish et al., 2004; Farley et al., 2007a) and can be the link between ocean conditions and juvenile sockeye salmon marine

survival on the eastern Bering Sea shelf (Farley et al., 2007c). Warm spring temperatures likely hasten lake ice break up, leading to earlier outmigration timing for Bristol Bay smolt. Thus, warm spring temperatures are advantageous to juvenile Bristol Bay sockeye salmon because these fish would spend more time in an ocean environment that is more conducive to rapid growth and offshore migration. The opposite would occur during years with cool spring temperatures.

What we do not understand is the magnitude of mortality either early on when juvenile sockeye salmon leave freshwater or after their first summer at sea. While over-winter mortality of juvenile salmon is speculated to be high if they do not reach a critical size over summer, we still do not know when this mortality event may take place as sockeye salmon spend more than one winter at sea. In addition, Farley and Trudel (in review) speculate that a continued rise in sea temperatures may actually decrease growth rate potential for juvenile sockeye salmon on the eastern Bering Sea shelf. Thus, while warmer sea temperatures during spring and summer have been shown to be advantageous to growth and survival of juvenile sockeye salmon within the range of historical observations, we still do not understand the effects of continued warming on the shelf and its impact on marine productivity and growth of juvenile salmon.

I believe that marine investigations of salmon are important to our understanding of salmon marine ecology, but collecting these data are at times difficult and expensive. Thus, agencies generally do not support long-term monitoring through expensive ocean surveys. Programs such as BASIS require a number of years of field sampling before associations between ocean environment and fish condition can be discerned. What W.F.

Thompson expressed about the Fisheries Research Institute back in the 1950s is true today for research programs embarking on marine surveys, "These programs take greater time developing their fruits than is the case with isolated academic problems because behind each paper lies a great mass of data secured over a period of years by an organization" (quote from Stickney, 1989).

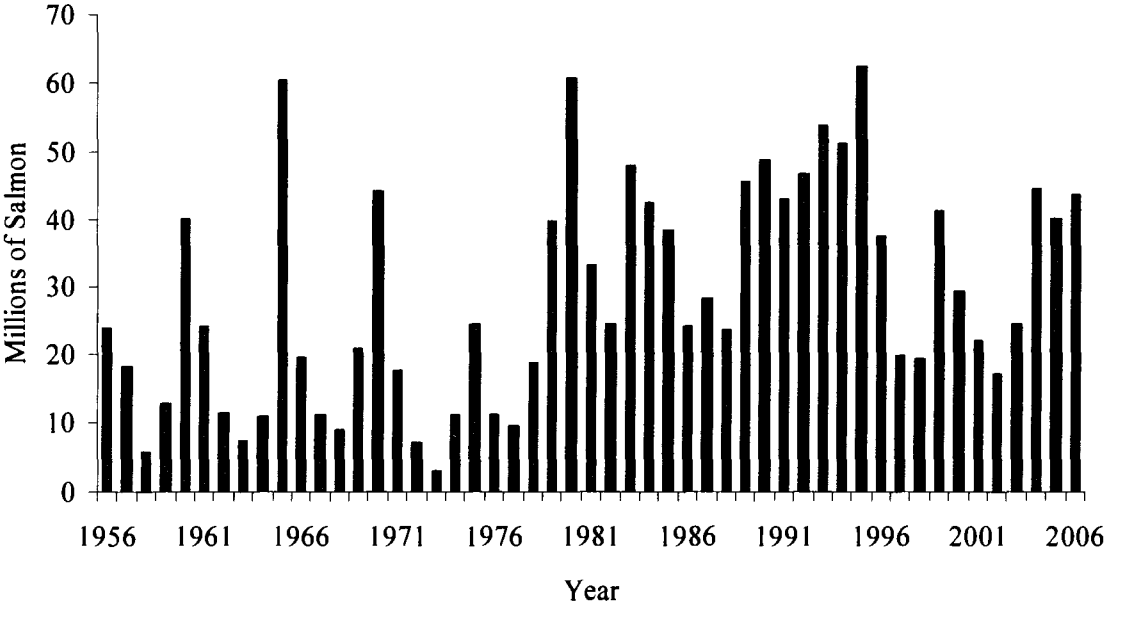

Figure 1.1. Total returns (millions) of adult Bristol Bay sockeye salmon 1956 – 2006. Data provided by L. Fair of ADFG Anchorage, Alaska.

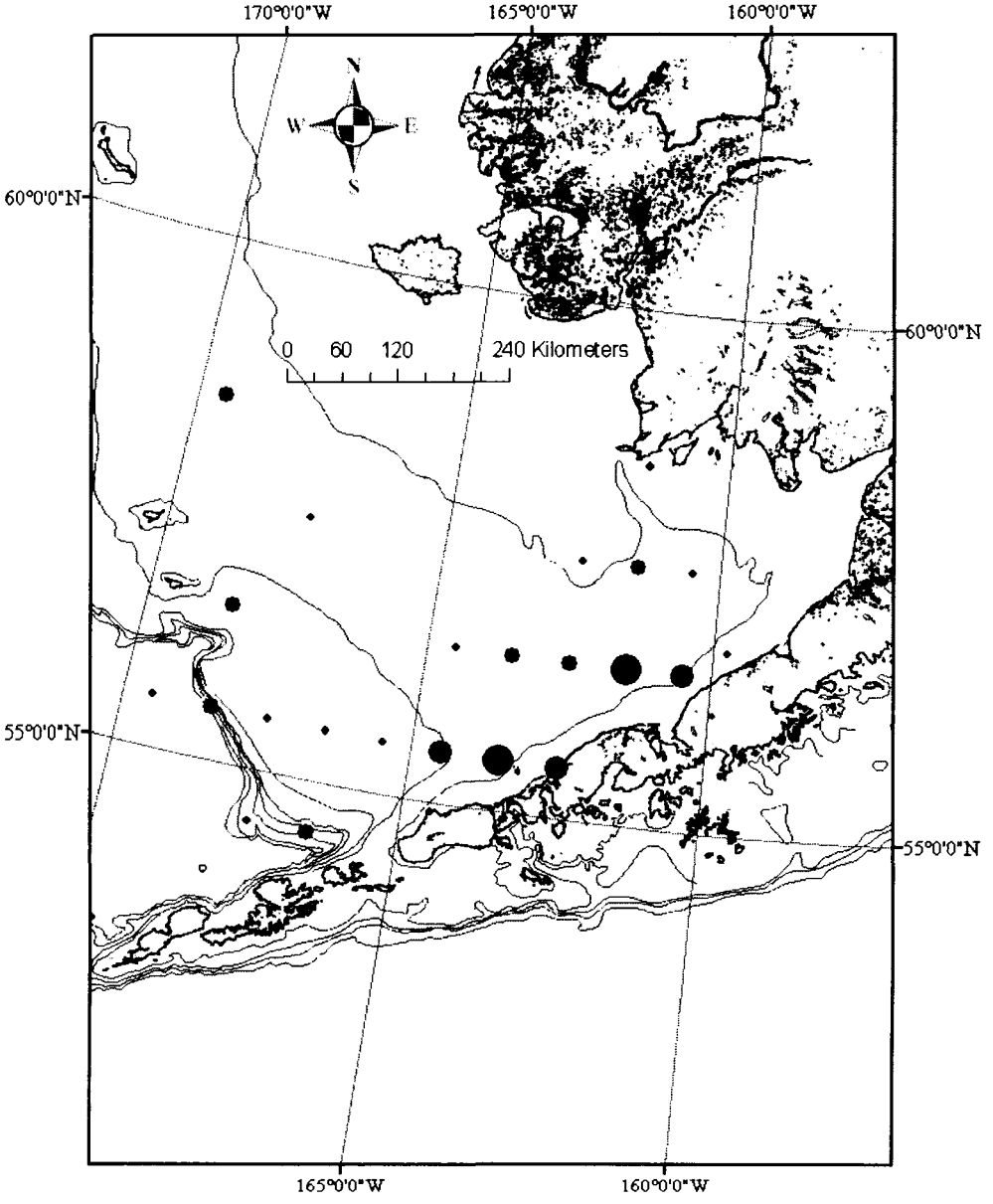

Figure 1.2. Area sampled by purse seine during 1964 to 1968 [shown by graduated symbol of number of stations sampled within a region; small dot = 1 to 4 stations; largest dot = 15 to 25 stations] (June to September) surveys of juvenile salmon along the eastern Bering Sea shelf by the University of Washington's Fisheries Research Institute (Hartt and Dell, 1986).

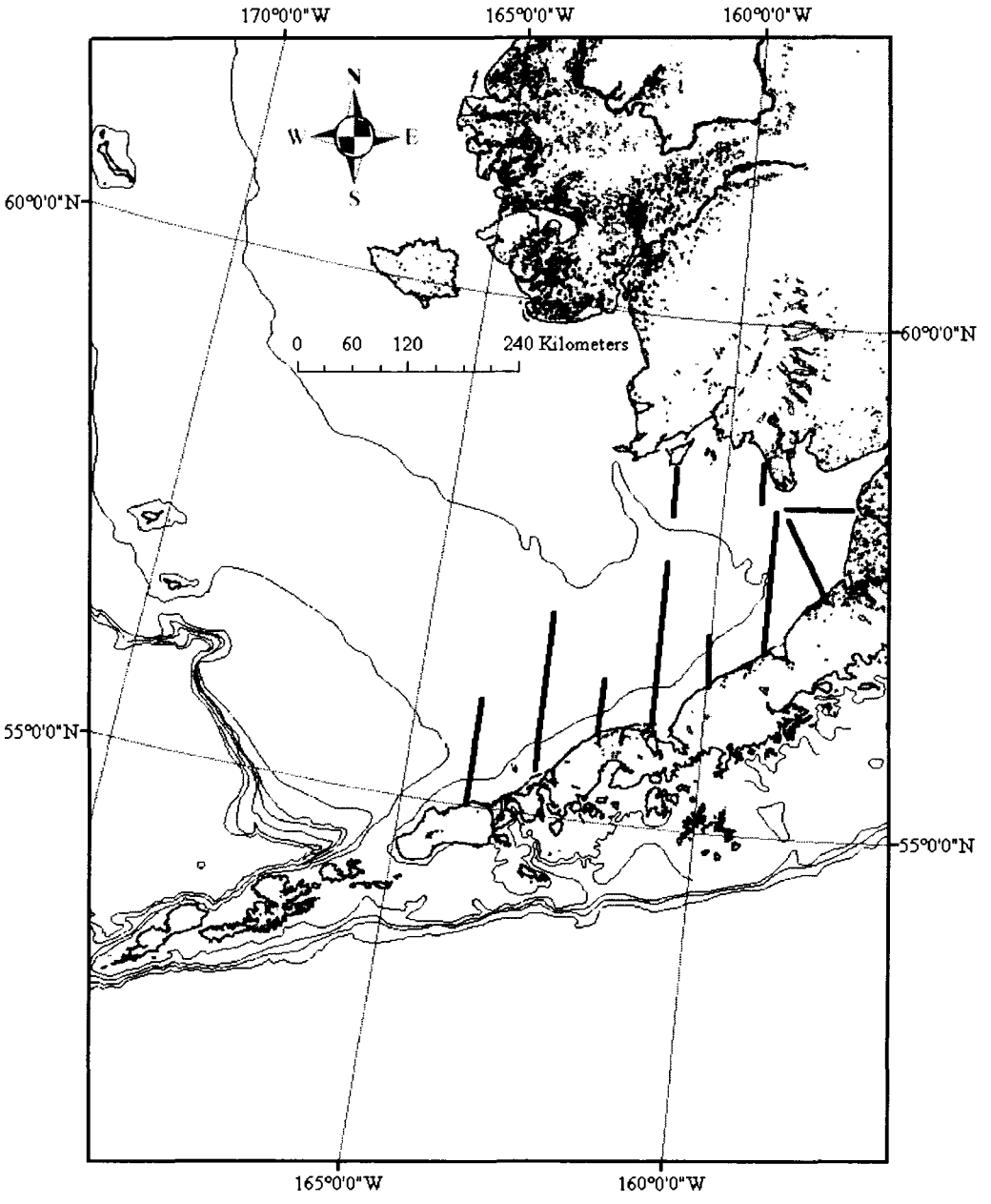

Figure 1.3. Transects sampled by purse seine during 1966 to 1972 (June to September) surveys of juvenile salmon along the eastern Bering Sea shelf by the US Fish and Wildlife Service (Straty, 1974; Straty and Jaenicke, 1980).

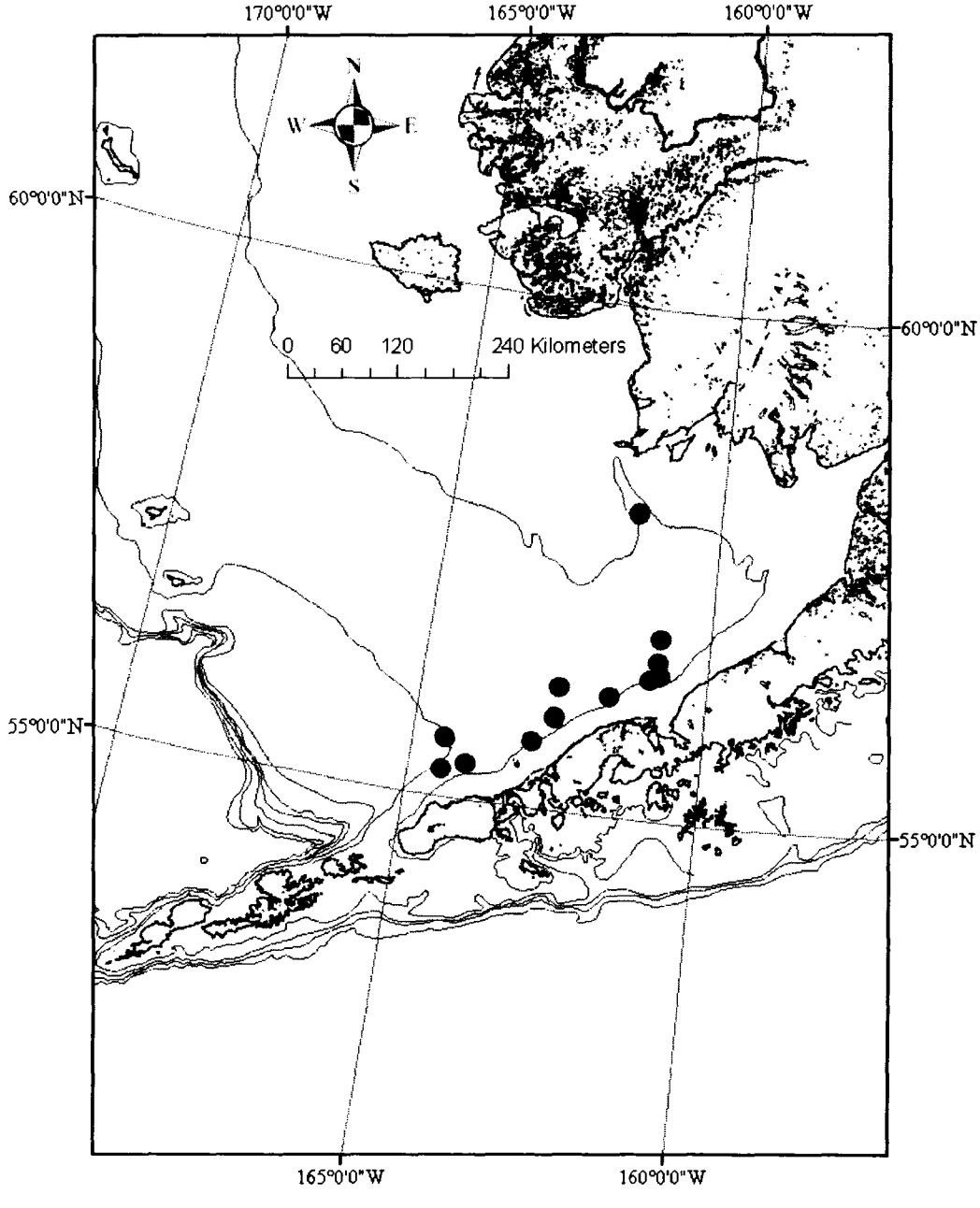

Figure 1.4. Stations (dots) sampled by variable-mesh gillnet during 1969 and 1970 (June to August) surveys of juvenile salmon along the eastern Bering Sea shelf by the Hokkaido University Faculty (Ogi, 1973).

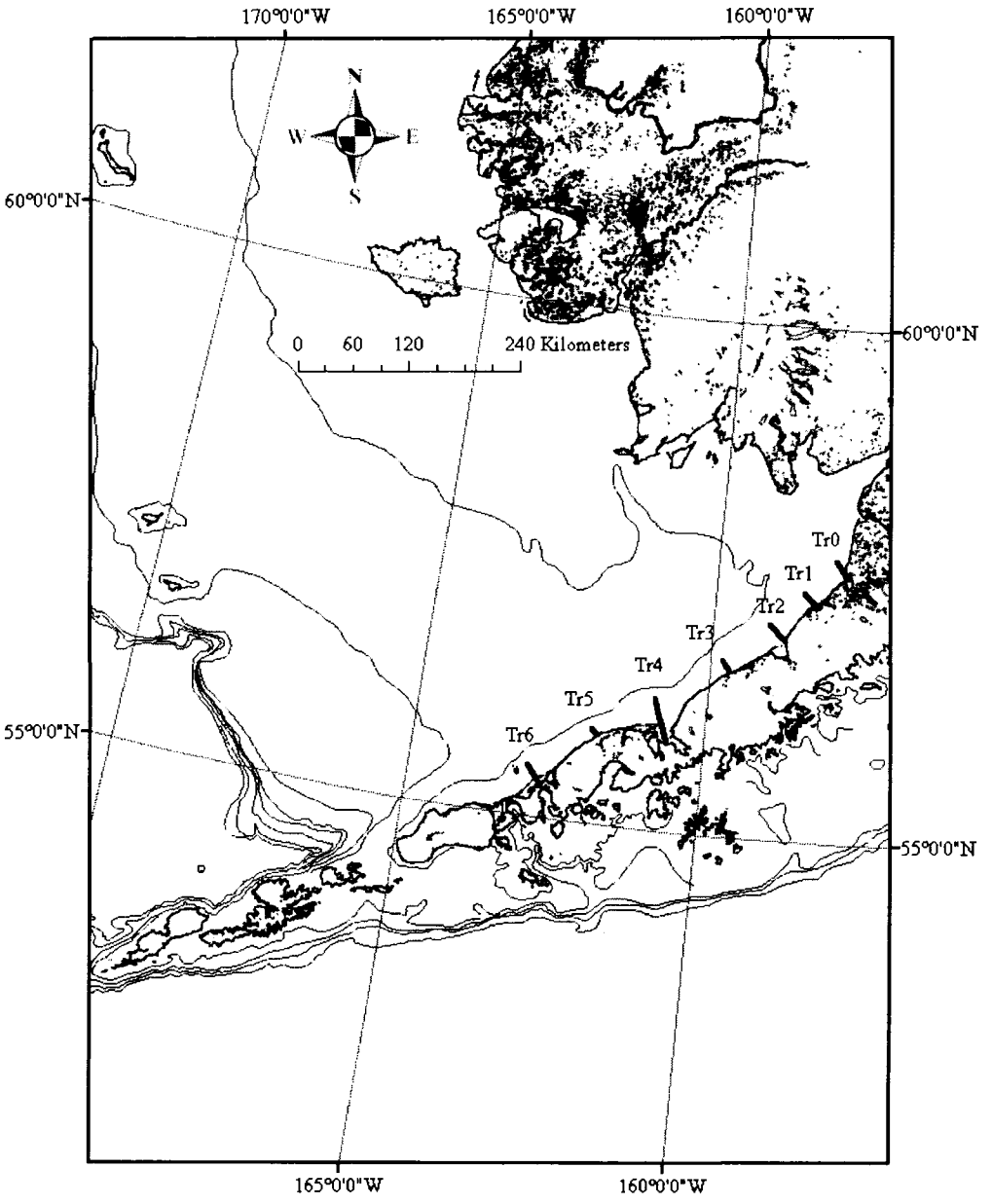

Figure 1.5. Transects sampled by purse seine during 1984 and 1985 (June to August) surveys along the eastern Bering Sea shelf by Dames and Moore and the Fisheries Research Institute, Outer Continental Shelf Environmental Assessment Program (Isakson et al., 1986).

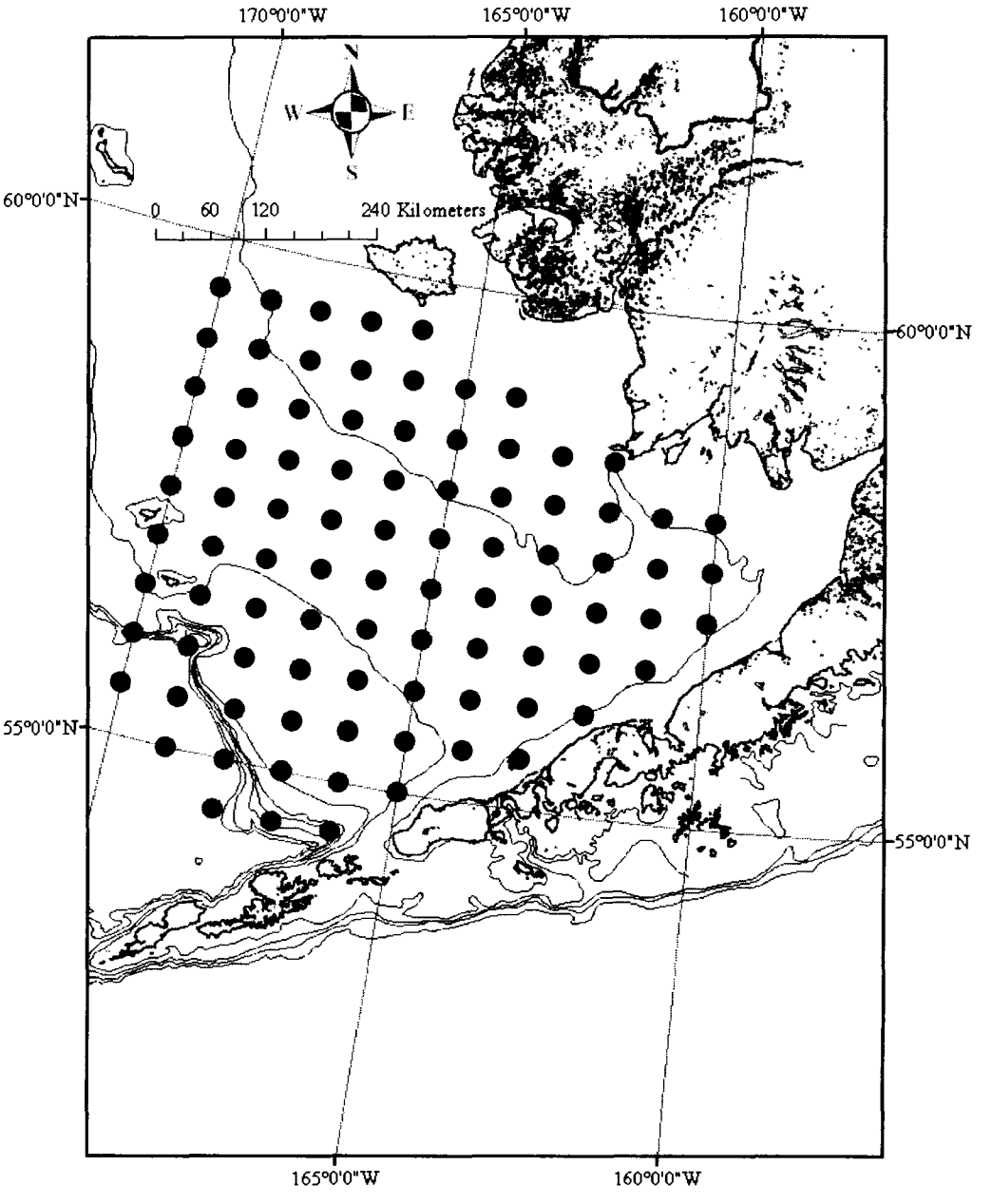

Figure 1.6. Stations (dots) sampled by rope trawl during 2002 to 2006 (August to September) surveys of juvenile salmon along the eastern Bering Sea shelf by the National Marine Fisheries Service, Alaska Fisheries Science Center, Bering-Aleutian Salmon International Survey (BASIS) Program. Stations during 2000 and 2001 offshore of 166W were not sampled.

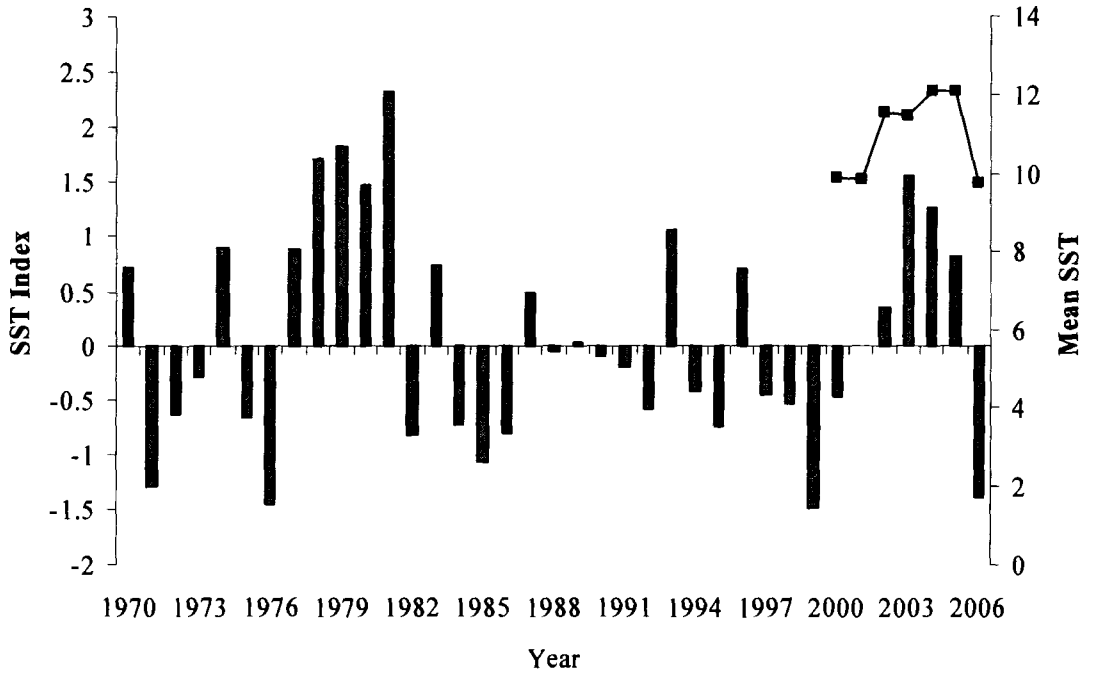

Figure 1.7. Indices of sea-surface temperatures (SSTs °C, bars) during May 1970 to 2006 in the southeastern Bering Sea (data courtesy of http://www.beringclimate.noaa.gov) and annual averages of SSTs (°C, box and line) during August to early September (2000 to 2006) during the Bering-Aleutian Salmon International Survey. Mean May SSTs are averaged over the area 54°18' N to 60°0' N, 161°12' W to 172°30' W using data from the NCEP/NCAR project (Kalnay et al., 1996). The index values are the deviations from the mean May SST value (2·33 °C) for the 1970 – 2000 period normalized by the standard deviation (0·76 °C). Mean August SSTs are the averages of SSTs at 5-m depth taken at stations conducted along the southeastern Bering Sea shelf by the Alaska Fisheries Science Center (see Farley et al., 2007b).

Table 1.1. Juvenile sockeye salmon indices of health during years with nearshore and offshore migration pathways from summaries of research by the Ocean Carrying Capacity Program 2000 to 2006.

	Migration Pathway		
Indices	Nearshore	Offshore	Reference
Size (Fork Length)	Smaller	Larger	1,2
Marine Survival	Lower	Higher	1
Gut Contents	Pacific sand lance, *euphausiids*	Age 0 pollock	2,3
Condition	Lower	Higher	2
Growth rate potential	Lower	Higher	4

[1]Farley et al. 2007c
[2]Farley et al. 2007b
[3]Farley, E. V., Jr., J. M. Murphy, J. Moss, A. Feldmann, and L. Eisner. In review. Juvenile western Alaska salmon research along the eastern Bering Sea shelf, August – October (2002 – 2006).
[4]Farley, E. V., Jr. and M. Trudel (in review). Growth rate potential of juvenile sockeye salmon in warm and cool years on the eastern Bering Sea shelf.

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2 EARLY MARINE GROWTH IN RELATION TO MARINE-STAGE SURVIVAL RATE FOR ALASKA SOCKEYE SALMON (*ONCORHYNCHUS NERKA*)[3]

2.1 Abstract

We tested the hypothesis that larger juvenile sockeye salmon (*Oncorhynchus nerka*) in Bristol Bay, Alaska have higher marine-stage survival rates than smaller juvenile salmon. We used scales from returning adults (33 years of data) and trawl samples of juveniles (n = 3572) collected along the eastern Bering Sea shelf during August through September 2000 – 02. The size of juvenile sockeye salmon mirrored indices of their marine-stage survival rate (e.g., smaller fish had lower indices of marine-stage survival rate). However, there was no relationship between the size of sockeye salmon after their first year at sea as estimated from archived scales and brood - year survival; size was relatively uniform over the time-series, possibly indicating size-selective mortality on smaller individuals during marine residence. Variation in size, relative abundance, and marine-stage survival rate of juvenile sockeye salmon is likely related to ocean conditions affecting their early marine migratory pathways along the eastern Bering Sea shelf.

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[3]Farley, E.V., Jr., J.M. Murphy, M.D. Adkison, L.B. Eisner, J.H. Helle, J.H. Moss, and J. Nielsen. 2007. Early marine growth in relation to marine-stage survival rate for Alaska sockeye salmon (*Oncorhynchus nerka*). Fishery Bulletin 105(1):121 – 130.

2.2 Introduction

Pacific salmon (*Oncorhynchus* spp.) experience relatively high mortality rates during the first few months at sea (Hartt, 1980), and it is believed that size plays an important role with larger fish having higher survival (Parker, 1968; Pearcy, 1992). Size-dependent mortality of juvenile salmon may be concentrated during two specific life history stages. The first stage may occur just after juvenile salmon enter the marine environment, where smaller individuals are believed to experience higher size-selective predation (Parker, 1968; Willette et al., 1999). The second stage is thought to occur following the first summer at sea, when smaller individuals may not have sufficient energy reserves to survive late fall and winter (Beamish and Mahnken, 2001). Thus, larger individuals likely have a higher probability of survival during both of these stages, emphasizing the importance of size and growth early on while salmon reside in the estuary and later during their first summer at sea.

Previous studies suggest that scale radius length is proportional to fish body length (Francis, 1990; Ricker, 1992) and, in particular, incremental increases in sockeye salmon (*O. nerka*) scale radius are strongly correlated with somatic growth (Fukuwaka and Kaeriyama, 1997). In this study, scales from adult Bristol Bay sockeye salmon were examined to determine the relationship between size after their first year at sea and survival to adulthood. We compared the time-series (1965-1997) of brood-year returns per spawner and scale growth measurements taken from adult sockeye salmon returning to the Egegik and Kvichak River systems in Bristol Bay, Alaska.

Juvenile sockeye salmon enter the marine waters of the eastern Bering Sea during May and June (Burgner, 1991) and migrate through Bristol Bay to the Bering Sea and North Pacific during the summer and early fall months (Straty, 1981; Farley et al., 2005). Two differing models of seaward migration are believed to exist for juvenile Bristol Bay sockeye salmon: in some years juvenile sockeye salmon migrate along the coastal waters of the eastern Bering Sea near the Alaska Peninsula, and in other years their migration is farther offshore (Farley et al., 2005). We also compared the size of juvenile Bristol Bay sockeye salmon collected during late summer and early fall (2000-2002) trawl surveys along the eastern Bering Sea shelf with indices of their abundance, marine-stage survival rate after our survey, and returns per spawner from these cohorts. Interannual differences in the size and growth rates of juvenile sockeye salmon were also compared to their early marine distribution and ocean conditions. The specific objectives of this study were to determine whether larger, presumably faster growing, juvenile sockeye salmon in fact had higher survival rates than smaller, presumably slower growing individuals, and what aspects of the marine environment might influence these growth rates.

2.3 Methods

2.3.1 Data

This research focused on Bristol Bay sockeye salmon because this region has the largest returns and commercial harvest of sockeye salmon in the world. Scales from adult sockeye salmon, salmon fork lengths, and brood-year return per spawner data for the Egegik and Kvichak Rivers in Bristol Bay, Alaska were obtained from the Alaska Department of Fish and Game (ADF&G). Salmon scales are collected annually by

ADF&G to estimate age composition of adult sockeye salmon for fishery management. Age was designated by the European notation, i.e., *a.b*, where *a* = the number of winters spent in freshwater prior to going to sea and *b* = the number of winters spent in the ocean (Koo, 1962a). Salmon scale collections and brood-year return per spawner data were available for the dominant freshwater and ocean age groups of sockeye salmon sampled in the Kvichak River (brood-year returns for ages 1.2, 1.3, 2.2, 2.3; 1965-1997) and the Egegik River (brood-year returns for ages 1.3, 2.2, 2.3; 1965-1997).

Scales were selected for measurement following procedures described in Ruggerone et al. (2005). Briefly, scales were selected when our age determination matched that previously made by ADF&G, the shape of the scale indicated that the scale was from the "preferred area" (below the dorsal fin and above the lateral line - see Koo, 1962b), and the circuli and annuli were clearly defined and not affected by scale regeneration or significant resorption along the measurement axis. The number of scale samples for each river system and age group are provided in Table 2.1.

Scales from adult sockeye salmon were digitized following procedures described by Hagen et al.[4] and Ruggerone et al. (2005). The scale measurement axis was determined by a perpendicular line drawn from a line intersecting each end of the first saltwater annulus. Distance (mm) between the focus and the outer edge of the scale was designated as the total scale length. The relationship between total scale length and adult fork length was linear for both the Egegik River (F-test, $P < 0.001$; $r^2 = 0.41$) and

[4] Hagen, P. T., D. S. Oxman, and B. A. Agler. 2001. Developing and deploying a high resolution imaging approach for scale analysis. Doc. 567, p. 11. North Pacific Anadromous Fish Commission, 889 Pender Street, Vancouver, Canada.

Kvichak River (F-test, $P < 0.001$; $r^2 = 0.36$) sockeye salmon samples. As an index of total growth through the first year at sea, we measured the distance from the focus to the outer edge of the first saltwater growth zone for each fish. A time-series of annual means of the individual growth during the first year at sea ($MSW1_{i,a,t}$) estimated for each adult freshwater age group (a represents 1 or 2) within a river system (i represents Egegik, Kvichak) was used as an index of size that sockeye salmon would have attained after their first year (t) at sea.

The total number of fish caught and the fork lengths (mm) of juvenile sockeye salmon within each trawl haul were recorded during the Bering-Aleutian Salmon International Survey (BASIS) research cruises along the eastern Bering Sea shelf during fall (August-September) 2000 to 2002 (Figure 2.1). The surveys were conducted over a broad area of the shelf and sampled the major oceanographic domains (coastal and middle; Kinder and Schumacher, 1981) along the eastern Bering Sea shelf. In addition, the surveys were designed to sample through the entire population of juvenile sockeye salmon from Bristol Bay lake systems to reduce the chance of sample variability that may affect our ability to interpret results for these salmon stocks. Recent descriptions of juvenile salmon migration pathways along the eastern Bering Sea shelf (Farley et al., 2005) and genetic stock composition indicate that juvenile sockeye salmon collected during the surveys were primarily from Bristol Bay.

Fish were collected using a mid-water rope trawl (see Farley et al., 2005 for description) rigged to sample the top 15m of the water column. We attempted to collect scales from juvenile sockeye salmon during all 3 years of the survey; however, sample

sizes of preferred scales were too small for statistical analyses due to descaling of the juvenile salmon by our mid-water rope trawl. Data collected during each trawl included the trawl speed and the height and width of the net opening using a Simrad FS900 (Simrad, Lynnwood, WA) net sounder. The mean date of collection of juvenile sockeye salmon sampled for length differed slightly between years (i.e., August 26 during 2000; September 5 during 2001; September 1 during 2002); lengths were adjusted to account for these differences.

2.3.2 **Analyses of survival and early marine-stage growth rates inferred from adult scales**

For each freshwater age group, we calculated an index of survival rate that normalized the data and removed possible density-dependent effects (i.e., Peterman et al., 1998; Mueter et al., 2002). Specifically, our index of survival rate was the time-series of residuals from a Ricker model defined by:

$$(1) \qquad \ln\left(\frac{R_{i,a.2,t+2} + R_{i,a.3,t+3}}{S_{i,t-(a+1)}}\right) = \alpha_{i,a} - \beta_{i,a} S_{i,t-(a+1)} + \varepsilon_{i,a,t}$$

where t is the first ocean year for sockeye salmon, S is the total number of spawners within river system i (i represents Egegik or Kvichak), R is the total return (catch + spawners) for each freshwater age group a (a represents freshwater age 1 or 2) within river system i, α and β are model parameters representing the number of recruits per spawner at low numbers of spawners and the level of density dependence (Quinn and Deriso, 1999), and $\varepsilon_{i,a,t}$ are the normally distributed residuals of the model. For our analysis, partitioning salmon brood-year productivity by fresh water age group was

necessary to directly compare our index of survival to our time-series of $MSW1_{i,a,t}$ growth.

Analysis of covariance (ANCOVA) was used to examine the effect of $MSW1_{i,a,t}$ on our indices of survival (see Figs. 2A and 2B for scatter plots of $\varepsilon_{i,a,t}$ and $MSW1_{i,a,t}$) with the addition of river system, age group, and year as factors in the model. The results suggested the year factor was highly significant (F-test, $P < 0.001$) and that $MSW1_{i,a,t}$ was not significant (F-test, $P = 0.18$). It was possible that during some years all fish could have had excellent growth and attained a large size, but the ANCOVA model would have attributed the large size to the highly significant year factor. However, when we removed the year factor from the ANCOVA model, $MSW1_{i,a,t}$ was less significant (*F-test*, $P = 0.27$). In addition, the residuals from these models contained significant positive autocorrelation.

Because our data contained significant autocorrelation and showed a time-series character, we created univariate time-series models (Wei, 1990) for both $MSW1_{i,a,t}$ and $\varepsilon_{i,a,t}$ to determine whether autoregressive or moving average components were present. The univariate models were developed by examining the sample autocorrelation and partial autocorrelation functions for each time-series. Time-series data were considered white noise processes, i.e., uncorrelated random variables with constant mean and variance, when none of the components of the sample autocorrelation and partial autocorrelation functions differed significantly ($P = 0.01$) from zero (Wei, 1990).

Multivariate time-series models in the form of linear transfer function (LTF) models (Liu and Hudak, 1992) were developed to describe the relationship between

$MSW1_{i,a,t}$ and our index of survival rate for each freshwater age group and river system. All of the univariate time-series of survival rate indices contained significant positive first order autoregressive parameters (see Table 2.2). Therefore, we included the first order autoregressive parameter in the LTF models. The models were defined as:

$$(2) \qquad \varepsilon_{i,a,t} = c_{i,a} + \lambda_{i,a} MSW1_{i,a,t} + \frac{1}{(1-\phi_{1,i,a}B)} N_{i,a,t}$$

where t, i, a, are described in Equation 1, $MSW1$ is the early marine growth index for sockeye salmon during their first year at sea, ϕ_1 is the autoregressive lag 1 parameter, B is the symbol for the backshift operator (i.e., $B^*S_t = S_{t-1}$), $c_{i,a}$ and $\lambda_{i,a}$ are parameters within the model, and $N_{i,a,t}$ is a sequence of random errors that are independently and identically distributed with a normal distribution. Parameters within the univariate and LTF models were deemed significant when their t-value was greater than 2.0 ($P < 0.05$). Autocorrelation analysis was used to examine whether the model residuals were white noise. Univariate and LTF models were compared using Schwartz's bayesian criterion (SBC; Wei, 1990) to determine if the inclusion of MSW1 in Equation 2 improved the model fit.

2.3.3 **Analyses of data from juveniles collected by trawling**

Next, we developed an index of relative survival rate of adult Bristol Bay sockeye salmon for 2000-2002, and indices of abundance and marine-stage survival rate of juvenile sockeye salmon collected during 2000 - 2002 to compare with mean lengths of juvenile sockeye salmon collected during those years. Relative survival was defined as the number of returning adult sockeye salmon from the brood-year escapements

contributing to the juvenile sockeye salmon in the trawl samples taken during years 2000, 2001, and 2002. For instance, juvenile sockeye salmon contributing to the early marine population during 2000 comprised age 2.0 fish from the 1997 and age 1.0 fish from the 1998 brood-year escapements, and these fish would have returned as adults during 2002 and 2003. Relative marine-stage survival rate (RS) was thus calculated as:

$$(3) \qquad RS_t = \frac{\sum_{a=1}^{2}(R_{a.2,t+2} + R_{a.3,t+3})}{(S_{t-2} + S_{t-3})/2}$$

where t is the year juvenile sockeye salmon were sampled (t = 2000, 2001, 2002), a is the freshwater age (1.0 or 2.0), R is the total number of returning adult sockeye salmon to Bristol Bay after year t, and S is the total number of spawners in Bristol Bay that contributed to the juvenile salmon population during year t. For instance, freshwater age 1.0 and 2.0 juvenile sockeye salmon sampled during 2000 came from cohorts spawning during 1998 (age 1.0) and 1999 (age 2.0) and returned as adults to Bristol Bay during 2002 for age groups 1.2 and 2.2 and during 2003 for age groups 1.3 and 2.3. The numbers of returning adult and spawning Bristol Bay sockeye salmon were estimated from brood-year return information provided by ADF&G.

Annual indices of juvenile sockeye salmon abundance (IA) were defined as:

$$(4) \qquad IA_t = (SA/ma)\bar{C}_t$$

where SA is the estimated survey area (189,000 km^2), $\overline{ma}$ is the mean area sampled by a trawl haul during the survey (distance traveled during the tow multiplied by the width of the net), and $\bar{C}_t$ is the mean number of juvenile sockeye salmon caught during year t (t = 2000, 2001, 2002). This formula would give the abundance of juvenile sockeye salmon in the survey area if we assumed that catchability using our mid-water trawl is 1, (i.e., all fish in front of the net are caught). Because this is unlikely, we treat our estimates as an index rather than the actual abundance. In fact, our juvenile sockeye salmon abundance indices were less than the resultant adult returns in some years, suggesting that catchability of the net is much less than 1. One study (Shuntov et al., 1993) that used larger surface trawl gear to sample juvenile salmon suggested that catchability of juvenile salmon was 0.3. We therefore divided our abundance indices by 0.3, although we still consider these values to be indices.

An index of juvenile sockeye salmon marine-stage survival rate (*IMS*) was estimated by:

$$(5) \qquad IMS_t = \frac{\sum_{a=1}^{2}(R_{a.2,t+2} + R_{a.3,t+3})}{IA_t} * 100$$

where R is defined above in Equation 3, IA_t is defined in Equation 4, t is the year juvenile sockeye salmon were sampled (t = 2000, 2001, 2002), and a is freshwater age (age 1.0 or 2.0).

These survival rate indices were correlated with the mean length of juvenile fish collected during the corresponding first year at sea. Because the dates in the survey area differed slightly among years (2000, August 20 – 31; 2001, August 29 – September 13; 2002, August 20 – September 14), we adjusted fish lengths to provide a standardized length using September 1, mid-date of the survey periods, as the standard date. Three different daily juvenile sockeye salmon growth rates were assumed: (1) 0 mm/day, representing no daily growth at sea, (2) 0.3 mm/day, the lower end of published ranges for juvenile Pacific salmon, and (3) 1.7 mm/day, representing the upper end of the range (see Fisher and Pearcy, 1988, 1990; Fukuwaka and Kaeriyama, 1994; Orsi et al., 2000 for daily growth rate ranges for juvenile Pacific salmon). Adjusted mean fish lengths (*MAL*) were calculated by:

$$(6) \qquad MAL_{t,j} = \frac{1}{n}\sum_{i=1}^{n}(GR_j * ND_{i,t} * L_{i,t} + L_{i,t})$$

where i is an individual fish sampled in year t, n is the sample size, j is the growth rate (either 0, 0.3, or 1.7), *ND* is the difference in days between the date the individual fish was sampled and September 1. *ND* was either negative or positive depending on if the day the individual sockeye salmon was sampled was before or after September 1.

Analysis of variance tests (ANOVA, fixed effect) were used to examine interannual differences in length. The independent variable in the ANOVA model

included year. Data were analyzed using S-Plus statistical software. If a significant difference ($P < 0.05$) occurred, a Sidak multiple comparison test was used to calculate the 95% ($\alpha = 0.05, 0.01, 0.001$) confidence intervals for all pairwise differences between the dependent variable means (Insightful, 2001). The level of significance between the pairwise differences was determined by examining those confidence intervals that excluded zero for the three values of α.

2.4 Results

2.4.1 Analyses of adult scale data

Examination of the autocorrelation and partial autocorrelation functions for Kvichak River freshwater age groups 1 and 2 and Egegik River freshwater age group 1 MSW1 univariate time-series indicated that these time-series had a constant mean and variance. For Egegik River freshwater age group 2 MSW1 growth index, the sample autocorrelation and partial autocorrelation functions indicated that a lag 1 autoregressive parameter was appropriate and the estimate of the parameter was significant (t-test, $P < 0.01$). Coefficients of variation were less than 4% for the MSW1 growth rate indices for each freshwater age group confirming the univariate model results that these time-series varied little over time. By comparison, the coefficients of variation for the time-series of returns per spawner for each freshwater age group were between 70% and 135%.

The MSW1 growth index was not significantly related to survival in any of the LTF models except Egegik freshwater age group 1 (Table 2.2). Parsimonious univariate models were reasonable explanations of survival for both river systems and age groups, having values of SBC nearly as low as the "best" models. The sample autocorrelation

and partial autocorrelation functions indicated that a lag 1 autoregressive parameter was appropriate for the all of the univariate survival rate time-series models. The estimates of the lag 1 autoregressive parameter were positive for all of the univariate models.

2.4.2 **Analyses of data from juveniles collected by trawling**

The distribution of juvenile sockeye salmon along the eastern Bering Sea varied among years (Figure 2.3). During 2000 and 2001, 75% of the total catch of juvenile sockeye salmon occurred south of 56° N, within the middle domain and south within the stratified waters near the coastal domain along the Alaska Peninsula. During 2002, 75% of the total catch of juvenile sockeye salmon occurred north of 57° N, with 50% of the total catch occurring north of 58° N within the shallow stratified waters near the northern coastal domain.

Significant differences in mean length (ANOVA, $P < 0.001$) for juvenile sockeye salmon occurred for all three growth rates (Table 2.3). The multiple comparison test indicated that average fork length of juvenile sockeye salmon was significantly larger during 2002 than during 2000 and 2001 for all three growth rates. Juvenile sockeye salmon collected during 2001 were significantly larger that those collected during 2000 for growth rates equal to 1.7 mm/day ($P < 0.001$). The rank order of juvenile sockeye salmon fork lengths was the same under growth rates of 0.0 and 0.3 mm/day, with the largest fish in 2002 and the smallest in 2001. For growth rates of 1.7 mm/day, the rank order from smallest to largest juvenile sockeye salmon was 2000, 2001, and 2002.

The indices of marine-stage survival rate and abundance mirrored the observed variation in fish fork length for growth rates of 0 and 0.3 mm/day; they were highest

during 2002 and at or near their lowest during 2001 (Table 2.4). In addition, the nearshore distribution of juvenile sockeye salmon (2001; Figure 2.3) appears to coincide with lower indices of abundance and marine-stage survival rate, whereas fish distributed in the northern area of our survey (2002; Figure 2.3) exhibited higher marine-stage survival rate and abundance.

2.5 Discussion

Our study indicates that the size of Bristol Bay sockeye salmon after their first year at sea is not directly related to their survival, when size is measured from growth rings on the scales of adults returning to the Egegik and Kvichak rivers. Analyses of this MSW1 growth index indicated that most of the time-series had a constant mean and variance. Similar studies that used adult scales from Atlantic (*Salmo salar* L.; Crozier and Kennedy, 1999), coho (*O. kisutch*; Briscoe, 2004), and chum (*O. keta*; Helle, 1979) salmon to measure growth (size) during their first year at sea found survival rate of a cohort was statistically unrelated to variation in growth (size) of these salmon. The relative uniformity in the size of salmon after their first year at sea and the lack of relationship between size and survival rate is contrary to the prevailing paradigm that the size achieved by fish after their first summer at sea is important to survival (Beamish and Mahnken, 2001). However, these results do not necessarily invalidate this paradigm; it is possible that the adult scale samples available for analysis only reflect those juvenile salmon that had attained sufficient size in order to survive to adulthood, and not those that died at sea (Crozier and Kennedy, 1999).

In support of this possibility, when we directly measured the fork length of juvenile sockeye salmon (Tables 2.3 and 2.4) during late summer and early fall surveys along the eastern Bering Sea shelf (2000–2002), smaller fish for daily growth rates of 0.0 and 0.3 mm/day had lower indices of marine-stage survival rate. This result is consistent with other studies of teleost fish, where larger individuals gain a survival advantage over smaller conspecifics during the juvenile life history stage (Parker, 1968; Healey, 1982; Holtby et al., 1990; Pearcy, 1992; Sogard, 1997; Mortensen et al., 2000; Beamish and Mahnken, 2001; Moss et al., 2005). This result is also in accord with the critical-size and critical-period hypothesis that proposes brood-year survival is determined by the number of juvenile salmon that have reached a critical size by the end of their first marine summer (Beamish and Mahnken, 2001; Beamish et al., 2004). The assumption of this hypothesis is fish that do not reach a critical size after their first summer at sea will die because they are unable to meet minimum metabolic requirements during late fall and winter (Beamish and Mahnken, 2001). While our results indicate larger juvenile sockeye salmon have higher relative marine-stage survival rate after their first year at sea, it is difficult to directly address when the mortality would occur, as sockeye salmon can spend an average of 2 to 3 years at sea. However, the overwhelming evidence from field and laboratory studies of juvenile stages of teleost fishes suggests that size-selective mortality occurs during winter, because larger members of a cohort can better tolerate physical extremes and endure longer periods without food (Sogard, 1997).

One other test of the critical size and critical period hypothesis is that mortality rates after this period should be large relative to other sources of early marine mortality

(Beamish et al., 2004). To interpret our indices of marine-stage survival rate as the actual post-survey marine survival requires making a variety of questionable assumptions (e.g., known vulnerability of juvenile salmon to our gear). However, if our estimates are close to correct, they would indicate that marine mortality rates of juvenile sockeye salmon may be greater than 70% (Table 2.4) after our late summer-early fall surveys. These marine mortality rates are substantial, and approach late fall and winter mortality rates of greater than 90% found for other Pacific salmon (Beamish et al., 2004).

Lengths of juvenile sockeye salmon differed significantly among years for all three daily growth rates. Differences in fork length of juvenile sockeye salmon could reflect annual differences in early marine growth rates or might also reflect annual differences in the size of smolt leaving Bristol Bay lake systems that is maintained during the summer growing season. However, limited surveys of sockeye salmon smolt from the Kvichak and Ugashik Rivers during 2000 through 2002 (Egegik River smolts were not during 2002) by ADF&G suggest that differences in smolt length among years and within age classes and river systems were less than 9%. In addition, the smallest average smolt size among these three years was seen during 2002, the year with the largest juvenile sockeye salmon size. Thus, it is likely that annual differences in length observed during our survey were due to differences in marine growth rates between years.

The annual variability in juvenile sockeye salmon size and indices of marine-stage survival rates may be linked to their early marine migration along the eastern Bering Sea shelf. Although we only had three years of data, size and survival indices of Bristol Bay sockeye salmon were lowest when juvenile sockeye salmon were distributed

nearshore along the Alaska Peninsula (i.e., the coastal migration pathway) and highest when they were distributed farther north and offshore. In support of this theory, the coastal migration pathway of juvenile Bristol Bay sockeye salmon observed by Straty (1981) during the late 1960s and early 1970s coincided with significantly lower production of Bristol Bay sockeye salmon that occurred prior to the mid 1970s (Adkison et al., 1996).

The annual variability in seaward migration pathways is likely related to ocean conditions on the shelf during spring and summer. Recent studies suggest that sea surface temperatures along the eastern Bering Sea in summer, the period when juvenile sockeye salmon are present on the shelf, is positively correlated with Bristol Bay sockeye salmon survival rates (Mueter et al., 2002). It is possible that the effect of sea surface temperatures on survival rates of juvenile Bristol Bay sockeye salmon is a result of its influence on early marine distribution of juvenile sockeye salmon. For example, during the late 1960s and early 1970s, the nearshore migration of juvenile Bristol Bay sockeye salmon was thought to be a result of sockeye salmon using the warmer nearshore waters rather than the colder sea surface temperatures offshore in order to maximize their growth (Straty, 1981). Depth-averaged sea temperatures from an oceanographic mooring along the eastern Bering Sea middle shelf domain for mid July to mid September were consistently warmer during 2001 and 2002 than during 1995 through 1997 (Overland and Stabeno, 2004). Presumably, the warmer sea temperatures during 2001 would have been conducive to offshore migration of juvenile sockeye salmon during that year. While sea temperatures were warmer during 2001 through 2002, sea temperatures along the shelf

were 1° to 2° C cooler from late June to September during 2001 than during 2002 (Overland and Stabeno, 2004). Thus, it may be that warmer sea temperatures during the time juvenile sockeye salmon first occupy the eastern Bering Sea shelf (beginning in June) provide a conduit for rapid offshore migration (and possibly higher survival) and that cooler sea temperatures delay offshore migration.

Our results suggest that after the first summer in the Bering Sea, larger juvenile sockeye salmon may gain a survival advantage over smaller individuals. This result, coupled with previous findings of reduced juvenile-to-adult survival of smaller pink (Moss et al., 2005) and coho (Beamish et al., 2004) salmon spending their first summer in the coastal waters of the Gulf of Alaska and Strait of Georgia, indicate that reduced growth of Pacific salmon during their first year at sea may lead to substantial salmon mortality, presumably during their first winter at sea. This phenomenon might not be seen if size of the salmon after their first year at sea is inferred from the scale growth increments of returning adults, as these individuals could be a biased sample from the faster-growing component of the population (Crozier and Kennedy, 1999). We suggest that annual variability in the size of sockeye salmon may be related to summer sea surface temperatures along the eastern Bering Sea shelf as a result of its influence on their spatial distribution and early marine migration pathways.

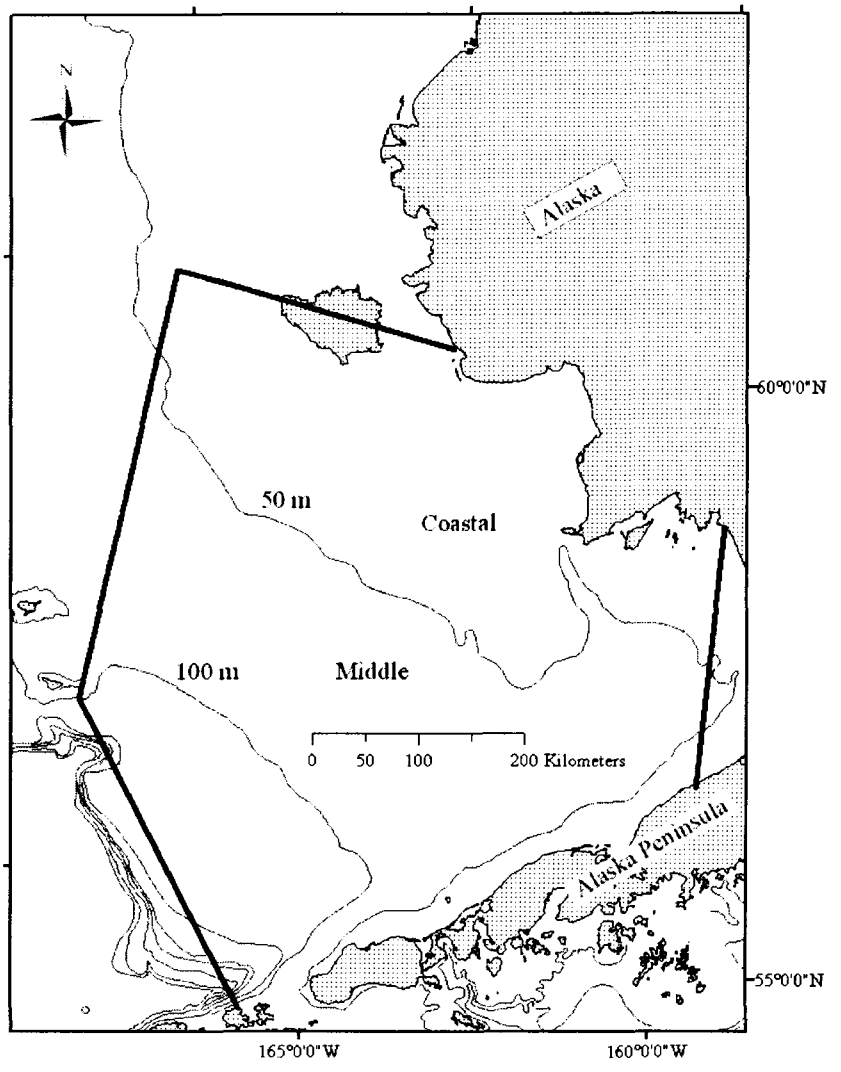

Figure 2.1. Survey area during the annual August-September (2000-2002) Bering-Aleutian Salmon International Survey (BASIS) within the coastal and middle domains of the eastern Bering Sea.

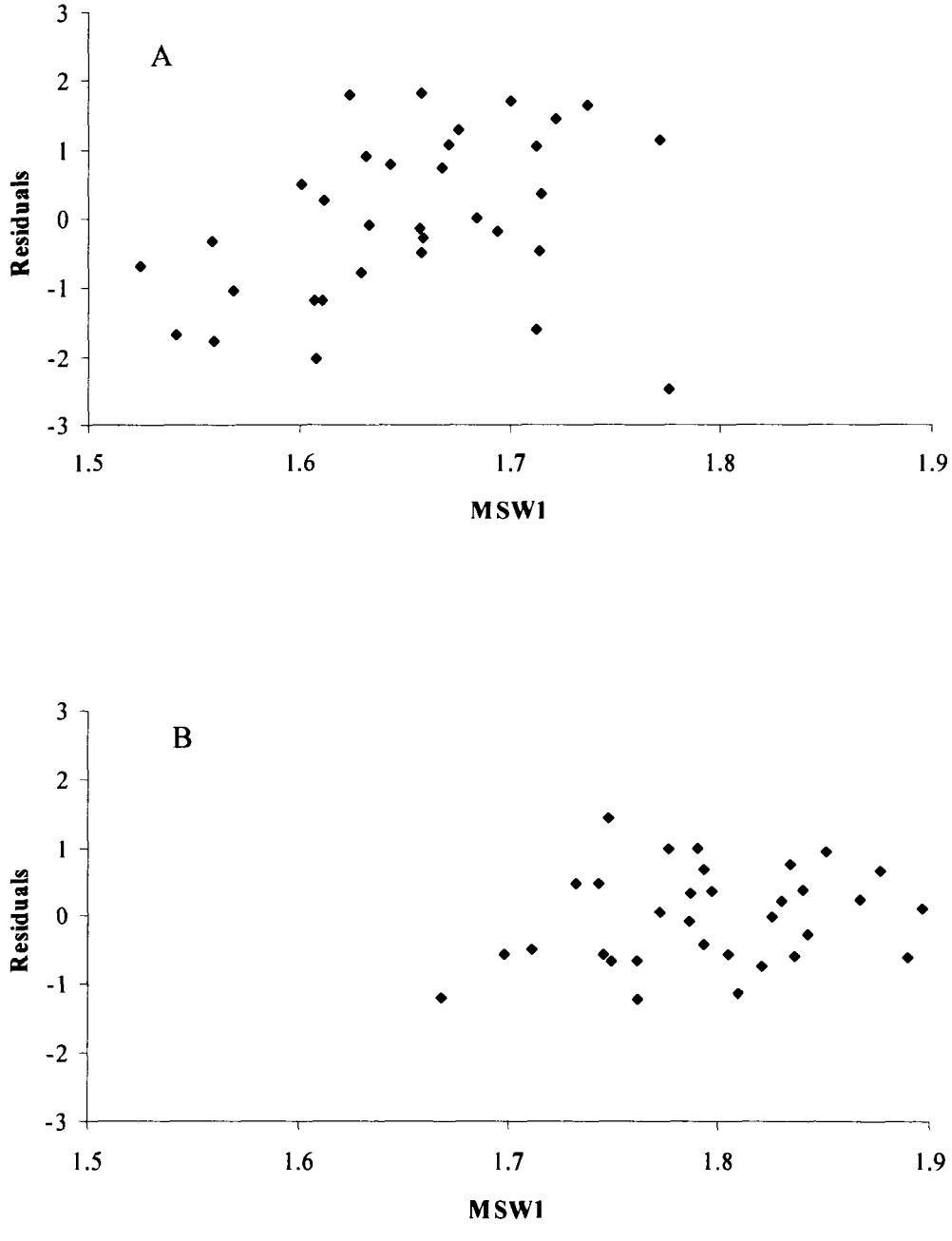

Figure 2.2. The relationship between the index of marine-stage survival rate (Residuals) and growth (*MSW1*) after the first year at sea for Egegik freshwater age groups 1 (A) and 2 (B) and Kvichak freshwater age groups 1 (C) and 2 (D) sockeye salmon (*Oncorhynchus nerka*).

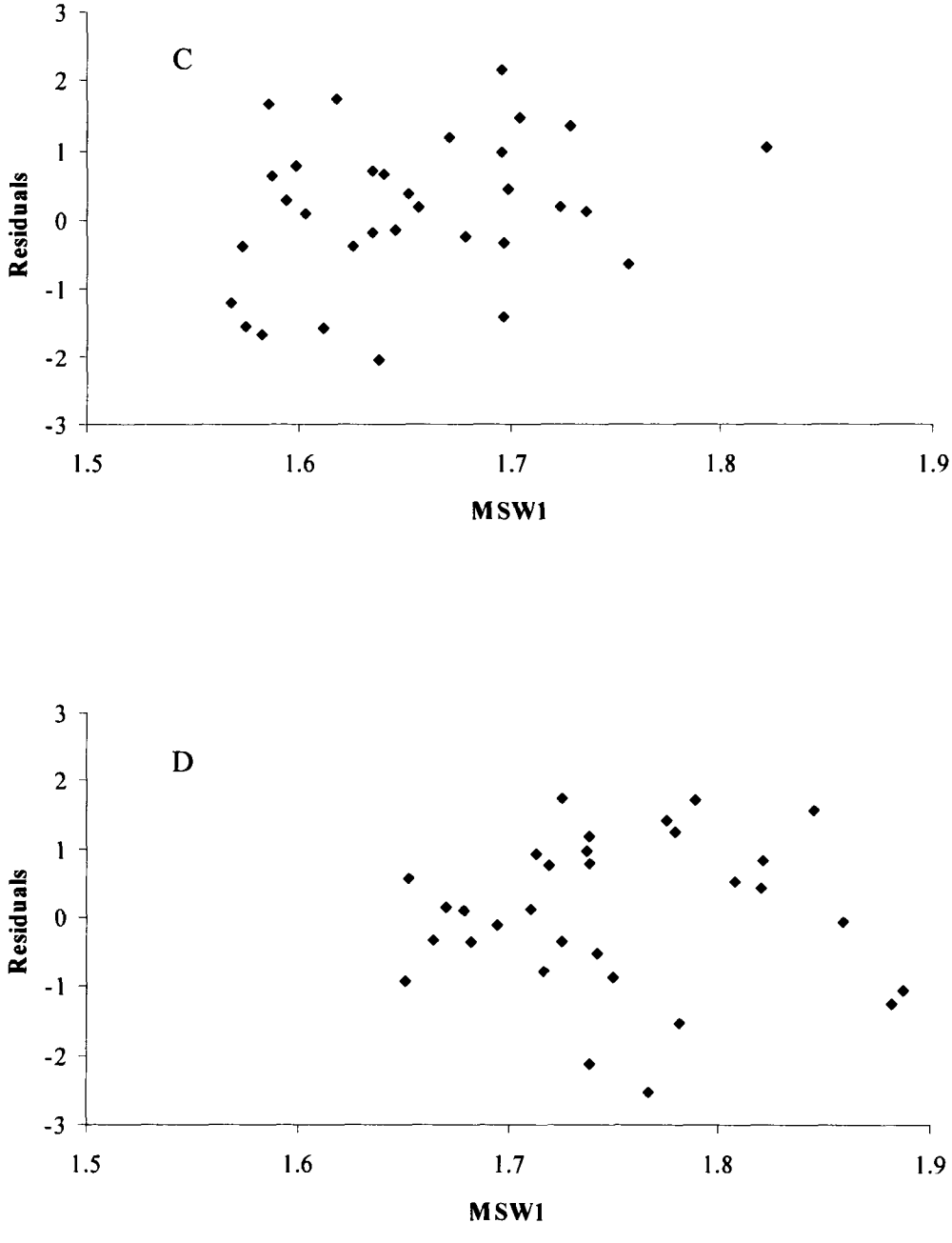

Figure 2.2 (continued). The relationship between the index of marine-stage survival rate (Residuals) and growth (*MSW1*) after the first year at sea for Egegik freshwater age groups 1 (A) and 2 (B) and Kvichak freshwater age groups 1 (C) and 2 (D) sockeye salmon (*Oncorhynchus nerka*).

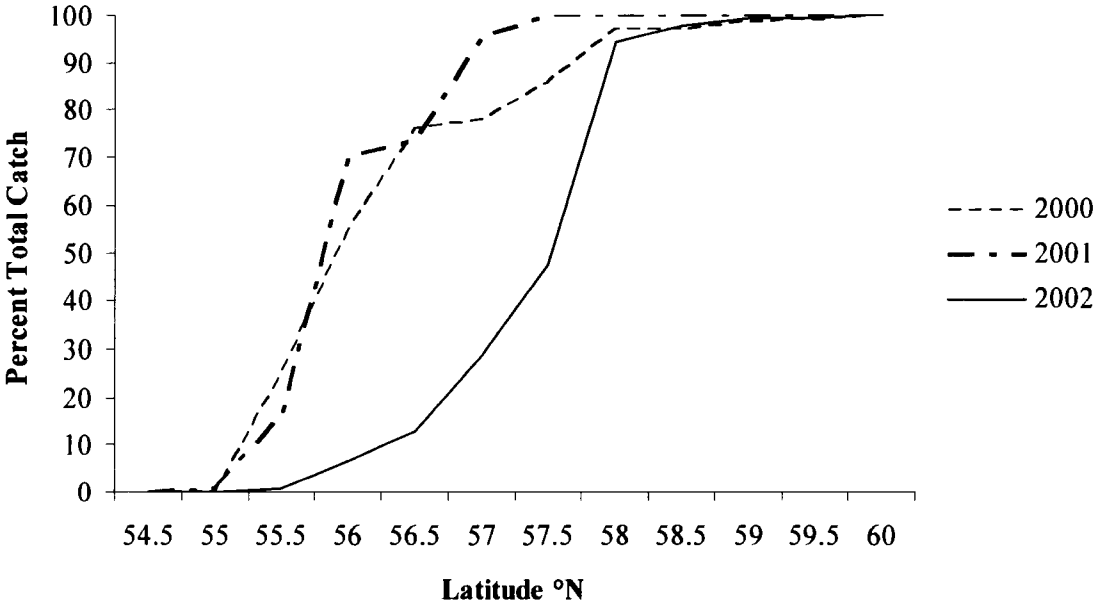

Figure 2.3. The percent of total catch of juvenile sockeye salmon (*Oncorhynchus nerka*) in relation to latitude (°N) along the eastern Bering Sea shelf during August-September 2000, 2001, and 2002.

Table 2.1. The total number of adult sockeye salmon scale samples for brood-years 1965-1997 for the Egegik and Kvichak River systems in Bristol Bay, Alaska. Age groups include 1.2, 1.3, 2.2, and 2.3.

	Age group			
River	1.2	1.3	2.2	2.3
Egegik	0	1265	1592	1581
Kvichak	1563	1441	1582	1246

Table 2.2. Univariate (Univ) and linear transfer function (LTF) models indicating the effect of early marine growth index (*MSW1*) on the index of marine-stage survival rates for each freshwater age group of sockeye salmon returning to the Egegik and Kvichak Rivers. Other variables include the constant (*Const*) and the autoregressive parameter ϕ_1. Model statistics include the number of effective observations (n), the coefficient of variation (R^2), residual standard error (*RSE*), the number of parameters (M), and Schwartz's Bayesian Criterion (*SBC*).

								Model coefficients			*t*-value		
River	Age	Model	n	R^2	*RSE*	M	*SBC*	*Const.*	*MSW1*	ϕ_1	*Const.*	*MSW1*	ϕ_1
Egegik	1	Univ	32	0.34	0.958	2	4.19	0.13	-	0.48	0.40	-	3.37
		LTF	32	0.41	0.908	3	4.22	-10.38	6.36	0.30	-2.22	2.25	2.07
	2	Univ	32	0.17	0.630	2	-22.64	0.02	-	0.42	0.10	-	2.64
		LTF	32	0.25	0.601	3	-22.19	-6.61	3.69	0.41	-1.74	1.75	2.59
Kvichak	1	Univ	32	0.29	1.075	2	11.56	-0.15	-	0.54	-0.36	-	3.60
		LTF	32	0.29	1.074	3	14.97	1.06	-0.73	0.54	0.21	-0.24	3.62
	2	Univ	32	0.35	0.986	2	6.00	-0.32	-	0.64	-0.64	-	3.99
		LTF	32	0.35	0.985	3	9.43	0.71	-0.59	0.64	0.18	-0.26	3.98

Table 2.3. Average fork length of juvenile sockeye salmon collected along the eastern Bering Sea during 2000, 2001, and 2002 assuming daily growth (mm) of 0, 0.30, and 1.7. Statistics include sample size (*n*), average fork lengths, and standard error (SE).

Juvenile Year	*n*	Average fork length (mm) 0	SE	0.3	SE	1.7	SE
2000	865	174.98	0.69	173.22	0.69	165.02	0.66
2001	804	171.67	1.27	172.97	1.30	179.05	1.44
2002	1918	192.13	0.76	191.63	0.79	189.26	0.95

Table 2.4. Indices of abundance (*IA*), marine-stage survival rate (*IMS*), and relative marine-stage survival rate (*RS*) for juvenile sockeye salmon collected along the eastern Bering Sea during 2000, 2001, and 2002.

Juvenile year	*IA*	*IMS*	*RS*
2000	130	21%	3.8
2001	137	15%	1.9
2002	180	34%	6.0

2.6 Literature cited

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3 JUVENILE SOCKEYE SALMON DISTRIBUTION, SIZE, CONDITION, AND DIET DURING YEARS WITH WARM AND COOL SPRING SEA TEMPERATURES ALONG THE EASTERN BERING SEA SHELF[5]

3.1 ABSTRACT

Interannual variations in distribution, size, indices of feeding and condition of juvenile Bristol Bay sockeye salmon *Oncorhynchus nerka* collected in August – September (2000 – 2003) during Bering – Aleutian Salmon International Surveys were examined to test possible mechanisms influencing their early marine growth and survival. Juvenile sockeye salmon were mainly distributed within the southern region of the eastern Bering Sea, south of 57°0' N during 2000 and 2001 and farther offshore, south of 58°0' N during 2002 and 2003. In general, juvenile sockeye salmon were significantly larger ($P < 0{\cdot}05$) and had significantly higher indices of condition ($P < 0{\cdot}05$) during 2002 and 2003 than during 2000 and 2001. The feeding index was generally higher for age 1.0 sockeye salmon than age 2.0 salmon during all years. Among-year comparisons suggested that Pacific sand lance (*Ammodytes hexapterus*) were important components of the juvenile sockeye salmon diet during 2000 and 2001 (20% to 50% of the mean wet mass) and age 0 pollock (*Theragra chalcogramma*) were important components during 2002 and 2003 (50% to 60% of the mean wet mass). Warmer sea temperatures during

[5] Farley, E.V., Jr., J.M. Murphy, M.D. Adkison, L. Eisner. 2007. Juvenile sockeye salmon distribution, size, condition, and diet during years with warm and cool spring sea temperatures along the eastern Bering Sea shelf. Journal of Fish Biology 71:1145 – 1158.

spring and summer of 2002 and 2003 likely increased productivity on the eastern Bering Sea shelf, enhancing juvenile sockeye salmon growth.

3.2 INTRODUCTION

Investigations into the early marine ecology of Pacific salmon *Oncorhynchus* sp. have found that ocean conditions can significantly affect salmon survival, particularly during the first few months after leaving freshwater (Holtby *et al.*, 1990; Friedland, 1998; Beamish & Mahnken, 2001; Beamish *et al.*, 2004). The assumption is that marine survival of juvenile Pacific salmonids is likely a function of their early marine growth (Pearcy, 1992; Beamish & Mahnken, 2001; Moss *et al.*, 2005; Farley *et al.*, 2007). Growth-based mortality during the first year at sea is believed to occur during two phases (Beamish *et al.*, 2004). The first phase is assumed to be predation-based and occurs early after juvenile salmon enter the marine environment (Pearcy, 1992). The second phase occurs after the first summer growing season when slower growing individuals have a higher probability of mortality (Beamish *et al.*, 2004). Both phases are likely linked to ocean conditions (*i.e.* water temperature, food resources, light) where favourable conditions presumably enhance early marine growth.

Sea surface temperatures during spring and summer within regions that juvenile salmon migrate can be useful predictors in models of survival rates or recruitment of salmon (Friedland, 1998; Mueter *et al.*, 2002). Sea temperature is an important variable regulating salmon consumption and growth rates (Donaldson & Foster, 1940) and in regulating growth and production of their potential prey (*i.e.* zooplankton; Corkett &

McLaren, 1978; Huntley & Lopez, 1992). Thus, sea temperature may impact salmon early marine survival rates by enhancing or limiting the productivity of potential prey and/or the metabolic processes that influence their growth rates.

Recent analyses of juvenile Bristol Bay sockeye salmon *Oncorhynchus nerka* (Walbaum, 1792) indicated that larger juvenile sockeye salmon had higher marine survival rates (Farley *et al.*, 2007). Past summer and fall surveys of juvenile Bristol Bay sockeye salmon established that the southeastern Bering Sea shelf is an important corridor for juvenile Bristol Bay sockeye salmon ocean migration (Straty, 1974; Farley *et al.*, 2005). Two different migration pathways for juvenile Bristol Bay sockeye salmon have been observed. The first migration pathway is west in a narrow coastal band, nearshore along the coastal waters of the Alaska Peninsula (Straty, 1974). The second migration pathway is farther offshore along the northern and southern sides of Bristol Bay (Farley *et al.*, 2005). The size, relative marine survival, and relative abundance of juvenile Bristol Bay sockeye salmon was highest during 2002, a year with an offshore migration pathway and lowest during 2000 and 2001, years when juvenile sockeye salmon were distributed nearshore (Farley *et al.*, 2007). Differences in migration pathways for juvenile Bristol Bay sockeye salmon were assumed to be a function of spring and summer sea surface temperatures where cooler spring and summer sea temperatures were associated with the nearshore migration pathway and warmer spring and summer sea temperatures were associated with the offshore migration pathway (Farley *et al.*, 2005, 2007).

The objective of this study is to compare the distribution, size, feeding, and condition of juvenile sockeye salmon along the eastern Bering Sea shelf during two years with cooler spring (May) sea surface temperatures and with two years of warmer spring sea surface temperatures. The cool spring sea surface temperatures on the eastern Bering Sea shelf occurred during 2000 and 2001, whereas, warmer spring sea surface temperatures occurred during 2002 and 2003 (Figure 3.1). These comparisons expand the previous analyses (Farley *et al.*, 2007) by separating distribution and size of juvenile sockeye salmon into freshwater age groups and by including additional salmon indices of health and fitness. Differences in diet, relative feeding index, and condition factor will be discussed in relation to distribution, earlier analyses on growth and survival of juvenile Bristol Bay sockeye salmon, and in relation to oceanographic features along the eastern Bering Sea shelf.

3.3 MATERIALS AND METHODS

3.3.1 STUDY AREA AND SAMPLING

During August – September 2000 – 2003, stations along the eastern Bering Sea shelf from longitudinal meridians 159°0' W to 168°0' W and from the Alaska Peninsula to Nunivak Island were sampled (Figure 3.2). Juvenile sockeye salmon were collected following the methods described in Farley *et al.* (2005). Briefly, fish were collected using a mid-water rope trawl that was 198 m long, had hexagonal mesh in wings and body, and had a 1·2 cm mesh liner in the codend. The rope trawl was towed at 6·5 to 9·3 km h^{-1}, at or near surface, and had a typical spread of 55 m horizontally and 15 m vertically. Trawl

stations were sampled during daylight hours (0730–2100, Alaska Daylight Savings Time) and all tows lasted 30 min and covered 2·8 to 4·6 km. During 2001, sampling occurred within the survey area from the Alaska Peninsula to 58°0′ N. The reason for limiting the northern extent of sampling during 2001 was due to rapidly declining catch per unit effort of juvenile sockeye salmon as the survey moved north. At each trawl station, juvenile sockeye salmon were selected at random (maximum 50) for further analyses. Standard biological attributes, including fork length (L_F, nearest mm) and body mass (nearest g) of juvenile sockeye salmon were measured onboard. To determine freshwater age, sockeye salmon scales were taken from the preferred (below the dorsal fin and above the lateral line - see Koo, 1962) or from a non – preferred area (when no preferred scales were available) and placed on numbered gum cards. Juvenile sockeye salmon were frozen (-80° C) and transported to the laboratory. In the laboratory, stomachs were removed from a sample of approximately 10 juvenile sockeye salmon from each trawl station. Individual stomachs were preserved in 10% formalin and placed in an individually labeled vial.

In the laboratory, gum cards containing juvenile sockeye salmon scales were pressed and their impressions transferred to 7·6 × 12·7 cm sheets of acetate. These impressions were magnified on an Indus microfiche reader, and a digital image was taken with a Screenscan high resolution scanner mounted directly to the reader's screen. Each image was digitized at 48 X magnification and a resolution of 14 megapixels. Scale images were subsequently imported into Optimas 6·5 for analysis and freshwater age was determined by examining circuli spacing and growth patterns on the scale (see Mosher,

1968). A subsample (approximately 25%) of sockeye salmon scales were aged by a separate reader and compared for between reader agreement. Age was designated by the European notation, *i.e. a.b*, where a = the number of winters spent in freshwater prior to going to sea and b = the number of winters spent in the ocean (Koo, 1962). For juvenile sockeye salmon from the Bristol Bay region, freshwater age groups consist of age 0.0, 1.0 and 2.0, however, the two major freshwater age groups that make up nearly all the sockeye salmon seaward migrants entering Bristol Bay are age 1.0 and 2.0 (Straty, 1974). Total catch of juvenile sockeye salmon for each major freshwater age group was determined by multiplying the fraction of each age group within a trawl haul by the total number of juvenile sockeye salmon caught during a 30-minute trawl (hereafter referred to as CPUE).

For stomach content analyses, individual stomachs were removed from vials, then the contents were removed and excess moisture was blotted with paper toweling. Material that was obviously composed of parasites, stomach lining, rocks, or any other non-prey items was removed. The stomach contents were weighed to the nearest 1·0 mg and recorded as stomach content mass. Prey items in the stomach contents were teased apart and categorized to the lowest possible taxonomic level. Contents for each prey category within an individual stomach were weighed to the nearest 1·0 mg.

3.3.2 INDICES OF CONDITION AND FEEDING

A condition index was used to indicate the relative growth of juvenile sockeye salmon over a longer term than provided by the stomach content and relative feeding

indices. The condition index was calculated as the ratio of the mass of each fish to its expected mass based on the fork length-mass regression for juvenile sockeye salmon (Perry *et al.*, 1996; see Farley *et al.*, 2005).

A feeding index (stomach content mass/wet mass of individual fish) for each age group was used to test for differences in stomach fullness between years. Fish stomach content mass may be a function of the number of fish in an area (density dependent feeding) and/or time of day. A regression analysis of feeding index as the dependent variable and CPUE and time of day as independent variables was performed with data from 1704 juvenile sockeye salmon (ages 1.0 and 2.0 combined for all years; y=0·032x_1 – 5·200 * $10^{-6}x_2$ – 0·006, r^2=0·150). The relative feeding index of juvenile sockeye salmon was determined as a residual from this regression line.

Diet composition, expressed as percent wet mass (%M), was used as the primary metric in the annual diet analyses and was calculated as: $\%M_{i,f} = M_{i,f}(\sum_i M_{i,f})^{-1} \cdot 100$, where, $M_{i,f}$ is the total mass of prey category i in the fth sockeye salmon stomach sampled for diet analysis. Stomach contents were divided into major groups including Pacific sand lance *Ammodytes hexapterus* (Pallas, 1814), euphausiid, and age 0 walleye pollock *Theragra chalcogramma* (Pallas, 1814). For age 1.0 sockeye salmon, the %M of Pacific herring *Clupea pallasii* (Valenciennes, 1847) during 2002 and 2003 was greater than 5% and therefore was added to the list of prey groups for this age group. Two "other" categories were included and described by "other fish", composed of unidentified fish, and fish species that were less than 5% wet mass of the diet within each year (including cottids, herring (age 2.0 sockeye salmon only), *Sebastes* sp., and pleuronectids) and

"other zooplankton", composed of zooplankton species that were less than 5% wet mass of the diet (including amphipods, arthropods, chaetognaths, copepods, *Limacina* spp., and mysids) for each year.

Percent frequency of occurrence of each major prey group (%F) was calculated for each year, where the total number of juvenile sockeye salmon within each year that contained a particular prey group in their diet was divided by the total number of salmon sampled for diet within each year. The results indicated that the %F of the diet items in juvenile salmon stomachs had a similar trend to the percent wet mass. Therefore, figures of %F for prey groups were not included in the result section, but the percent frequency of occurrence of empty (%FE) juvenile salmon stomachs among years were included in Table 3.2.

Age 0 pollock and sand lance were captured in the trawl gear (Farley *et al.*, 2005). The present data indicated that the typical size range for age 0 pollock and sand lance in the trawl samples was between 45 and 95 mm total length (L_T) and 77 to 150 mm (L_F), respectively and that the typical size range of age 0 pollock and sand lance in the diets of juvenile sockeye salmon was between 28 to 67 mm (L_T) and 55 to 80 mm (L_F), respectively. There was a possibility that juvenile sockeye salmon could feed on age 0 pollock and sand lance during trawl operations (net feeding), however, observations on the state of digestion for these prey items in juvenile sockeye salmon stomachs generally indicated some degree of digestion. Cumulative frequency distributions of the percent total catch of juvenile sockeye salmon for each age group, age 0 pollock, and sand lance in relation to distance offshore (Latitudinal meridians in decimal degrees) of the Alaska

Peninsula were created to help in the discussion on the inter annual variation in distribution of juvenile sockeye salmon and their prey. The CPUE's of age 0 pollock and sand lance were also included to provide perspective on the relative abundance of these diet items for juvenile sockeye salmon.

3.3.3 STATISTICAL ANALYSIS

Analysis of variance tests (ANOVA, fixed effect) were used to examine interannual differences in length, mass, condition index, and relative feeding index. The independent variables in the ANOVA models included age group, year, and the interaction term between year and age group. Data were analyzed using S-Plus statistical software. If a significant difference ($P < 0{\cdot}05$) occurred, a Sidak multiple comparison test was used to calculate the 95% ($\alpha = 0{\cdot}05, 0{\cdot}01, 0{\cdot}001$) confidence intervals for all pairwise differences between the dependent variable means (Insightful, 2001). The level of significance between the pairwise differences was determined by examining those confidence intervals that excluded zero for the three values of α.

3.4 **RESULTS**

Distribution of juvenile sockeye salmon along the eastern Bering Sea shelf varied among years (Figures 3.3a and b). During 2000 and 2001, approximately 80% of the total juvenile sockeye salmon catch occurred between 55°0' N and 57°0' N, with the exception of age 1.0 sockeye salmon during 2000, where 80% of the catch occurred between 55°0' N and 58°0' N. In contrast, 80% of the total catch of age 1.0 and age 2.0 sockeye salmon

during 2002 and 2003 occurred between 56°0' N to 58°0' N and between 56°30' N to 58°0' N, respectively, indicating a shift in distribution of juvenile sockeye salmon that was offshore of the Alaska Peninsula and north during those years.

The size of juvenile Bristol Bay sockeye salmon increased each year for both age groups (Table 3.1). Mean L_F were significantly different between age groups ($F_{1,3627}$=714·26, P<0·001), among years ($F_{3,3627}$=165·09, P<0·001), and within the interaction of year and age group ($F_{3,3627}$=2·98, P=0·030). The pairwise comparison for the interaction among years indicated that mean L_F was significantly lower (P<0.001) during 2000 and 2001, when compared to 2002 and 2003 for both age groups. The pairwise comparison for the interaction between age groups indicated that mean L_F of age 2.0 sockeye salmon was significantly larger the age 1.0 during each year (P<0.01; 2000; P<0.001; 2001, 2002, 2003). Mean mass was also significantly different between age groups ($F_{1,3627}$=666·20, P<0·001), among years ($F_{3,3627}$=190·76, P<0·001), and within the interaction of year and age group ($F_{3,3627}$=11·36, P<0·001). The pairwise comparison for the interaction among years indicated that mean mass was significantly lower (P<0.001) during 2000 and 2001, when compared to 2002 and 2003 for both age groups. The pairwise comparison for the interaction between age groups indicated that mean mass of age 2.0 sockeye salmon was significantly larger (P<0.001) the age 1.0 during each year except 2000 (P>0.05).

The relationship between the natural log of L_F and mass of juvenile sockeye salmon was highly significant (y=3·220x – 12·670, r^2=0·99). Annual differences in mean condition index indicated that the index was lowest during 2000 and 2001 and highest

during 2002 and 2003 (Table 3.1). ANOVA indicated that condition index was significantly different by year ($F_{3,3627}$=18·54, P<0·001), age group ($F_{1,3627}$=7·10, P=0·008), and the interaction term of year and age group ($F_{3,3627}$=4·06, P=0·007). Pairwise comparisons for the interaction among years indicated that the condition index was significantly higher during 2002 (P<0.01; age group 1.0; P<0.001; age group 2.0) and 2003 (P<0.001) when compared to 2001 for both sockeye salmon age groups and significantly higher during 2002 (P<0.001) when compared to 2000 for age group 2.0 sockeye salmon. The condition index was generally higher for age 1.0 than age 2.0 sockeye salmon during each year. The pairwise comparison for the interaction between age groups indicated that condition of age 1.0 sockeye salmon was significantly higher (P<0.05) than age 2.0 during 2003.

The mean relative feeding index was lowest during 2000 and highest during 2003 for age 1.0 sockeye salmon and was highest during 2000 and 2001 for age 2.0 sockeye salmon (Table 3.2). ANOVA indicated that the relative feeding index was not significantly different among years (P=0·081) but was significantly different by age group ($F_{1,1699}$=6·75, P=0·009) and the interaction between age group and year ($F_{3,1699}$=3·02, P=0·009). In general, the feeding index was higher for age 1.0 sockeye salmon than for age 2.0. The pairwise comparison for the interaction between age group suggested that the feeding index was significantly higher for age 1.0 than for age 2.0 sockeye salmon during 2003 (P<0.01). The pairwise comparison for the interaction among years and between age groups indicated that the feeding index was significantly

higher during 2001 ($P<0.05$), 2002 ($P<0.01$), and 2003 ($P<0.01$) when compared to 2000 for age group 1.0 sockeye salmon.

Fish, including age 0 pollock, sand lance, and other fish dominated the diets in terms of percent wet mass of juvenile sockeye salmon (Figure 3.4). Among-year comparisons indicated that the percent wet mass of age 0 pollock in juvenile sockeye salmon diets increased from less than 50% during 2000 and 2001 to greater than 50% during 2002 and 2003 (Figure 3.4a). In contrast, the percent wet mass of sand lance in juvenile sockeye salmon diets was greatest during 2000 and 2001 (20% to 50%) and lowest during 2002 and 2003 (< 15%) (Figure 3.4b).

The %FE was greatest during 2000 and 2001 for age 1.0 sockeye salmon and similar across years (< 5%) for age 2.0 sockeye salmon (Table 3.2).

Annual distributions of dominant prey groups (age 0 pollock and sand lance) differed (Figure 3.5). Approximately 90% of the total catch of age 0 pollock occurred south of 57°0' N during 2000, 2001, and 2003; whereas during 2002, age 0 pollock were more evenly distributed across the eastern Bering Sea shelf (Figure 3.5a). Over 90% of sand lance was distributed south of 55°30' N, indicating a nearshore distribution along the Alaska Peninsula during 2001 and 2002 (Figure 3.5b). Sand lance had a bimodal distribution during 2000 with approximately 50% of the catch occurring south of 55°0' N and 50% of the catch occurring in the northern region of the survey area, north of 58°0' N. The mean CPUE of sand lance was highest during 2000 and declined during subsequent years, whereas the mean CPUE of age 0 pollock was lowest during 2000 and increased during subsequent years (Figure 3.6).

3.5 DISCUSSION

Juvenile sockeye salmon were significantly larger and had a significantly higher condition index during 2002 and 2003 (warmer sea temperature years) compared to 2000 and 2001 (cooler sea temperature years). Annual comparisons of juvenile sockeye salmon diet indicated a shift in primary prey from sand lance during 2000 and 2001 to age 0 pollock during 2002 and 2003. The distribution of juvenile sockeye salmon on the eastern Bering Sea shelf also varied. Juvenile sockeye salmon were mainly distributed from the Alaska Peninsula to 57°0' N during 2000 and 2001, but were distributed farther offshore of the Alaska Peninsula to 58°0' N during 2002 and 2003.

Previous research indicated that marine-stage survival of juvenile Bristol Bay sockeye salmon was highest during 2002 when compared to 2000 and 2001 (Farley *et al.*, 2007). Higher marine survival for Pacific salmon is believed to be linked to body size after the first summer at sea, where larger fish have a greater chance of survival during late fall and winter (Beamish & Mahnken, 2001). The present results suggest that juvenile sockeye salmon were larger and were in better condition during 2002 and 2003 than those fish caught during 2000 and 2001. Thus, the annual variations in size and condition index may be linked to marine-stage survival where fish that are large and in the best condition after their first summer at sea appear to have higher marine-stage survival.

Differences in fork length (size) of juvenile sockeye salmon could reflect annual differences in early marine growth rates or might also reflect annual differences in the

size of smolt leaving Bristol Bay lake systems. Limited surveys of sockeye salmon smolt from the Kvichak River and Ugashik River during 2000 through 2002 (Egegik River sampling was not done during 2002) by ADF&G suggest that differences in smolt L_F among these years and within freshwater age group and river systems were less than 9%. In addition, the smallest mean smolt L_F among these three years was seen during 2002, a year with large juvenile sockeye salmon size. Thus, marine growth rate, at least for juvenile sockeye salmon from these rivers, would have to have been higher during 2002 to compensate for smaller size sockeye salmon smolt during that year. One other possible explanation for increased growth during 2002 and 2003 could be the timing of seaward migration from freshwater lakes. Most sockeye salmon lakes are covered by ice in winter, and the salmon smolt usually begin their seaward migration within days of ice breakup (Burgner, 1991). Lake ice breakup was likely earlier in Bristol Bay during 2002 and 2003 due to warmer spring temperatures. Therefore, larger size of juvenile salmon during those years may reflect the longer time period in the marine environment (Rogers, 1988).

If size of juvenile salmon after their first summer at sea is linked to higher marine survival, then identifying the mechanisms involved in early marine growth and abundance of juvenile salmon is key to understanding their population dynamics and recruitment variability. Recently, a oscillating control hypothesis (OCH) was proposed that provides a conceptual framework for understanding decadal-scale changes in ocean climate and its importance to trophic structure on the eastern Bering Sea shelf (Hunt & Stabeno, 2002). The OCH predicts that during cold regimes, zooplankton prey for larval fish would be limited, negatively impacting recruitment of fish populations on the shelf.

In contrast, warm regimes are associated with strong zooplankton productivity and higher survival of larval and juvenile fish. Evidence from other studies suggests that the eastern Bering Sea shelf was warmer during 2002 and 2003 than the previous years (Overland & Stabeno, 2004). Zooplankton data were not available for productivity analyses on the shelf, but the warmer sea temperatures appear to coincide with increased relative abundance of age 0 pollock during 2002 and 2003 (Fig. 6a) and an increase in relative abundance and marine-stage survival of juvenile Bristol Bay sockeye salmon (Farley *et al.*, 2007). Therefore, the present results suggest that "warm regime" dynamics in the eastern Bering Sea could be associated with larger size and higher marine-stage survival of juvenile sockeye salmon and that these conditions may be the result of increased abundance of forage fish along the eastern Bering Sea shelf.

Because size after the first year at sea is important to survival of Pacific salmon, it would be conceivable to expect to see smaller fish compensating for their size by eating more food. Compensatory growth of smaller fish that were denied food occurs in Atlantic salmon (Young *et al.*, 2005) and some teleost fishes (Sogard & Olla, 2002), once food items are restored. The present results indicated that smaller age 1.0 sockeye salmon generally had higher relative feeding indices than age 2.0 sockeye salmon suggesting that these smaller fish had more food in their stomachs. In addition, the condition index of age 1.0 sockeye salmon was generally higher than age 2.0 sockeye salmon, suggesting that age 1.0 sockeye salmon were actively feeding at higher rates over a longer period of time. However, the smallest age 1.0 sockeye salmon found during 2000 and 2001 had the lowest feeding indices and the highest %FE. A likely explanation for this phenomenon is

that prey could have been a limiting factor to growth rates for age 1.0 sockeye salmon during 2000 and 2001.

Consumption of fish as prey by juvenile sockeye salmon on the eastern Bering Sea shelf appears to be unique. For example, in the western Bering Sea, juvenile sockeye salmon fed primarily on hyperiid amphipods (*Themisto pacifica*) during late fall (Radchenko & Mathisen, 2004); whereas juvenile sockeye salmon captured along the coastal Gulf of Alaska during August fed primarily on Euphausiacea (Auburn & Ignell, 2000). The present results indicated that during late August and early September, juvenile sockeye salmon primarily fed on Pacific sand lance and age 0 pollock. In addition, an earlier study on juvenile Bristol Bay sockeye salmon diet that occurred during June – September (1966 and 1967) indicated that these fish fed primarily on copepods; however Pacific sand lance did become an important component of the diet later on during their seaward migration (Carlson, 1976). There are large numbers of larval and juvenile fish on the eastern Bering Sea shelf in comparison to western Bering Sea (*i.e.* age 0 pollock; see Brodeur *et al.*, 1999). Thus, it is likely that juvenile Bristol Bay sockeye salmon are taking advantage of abundant upper trophic level larval and juvenile fish prey resources available to them on the eastern Bering Sea shelf.

The connection between ocean conditions and marine-stage survival of salmon on the eastern Bering Sea shelf is likely by means of the size and condition of the fish after their first summer at sea. Warmer sea surface temperatures during spring may be a surrogate to "warm regime" dynamics whereby the mechanism regulating size and

condition of juvenile salmon is bottom-up control of the trophic structure on the eastern Bering Sea shelf.

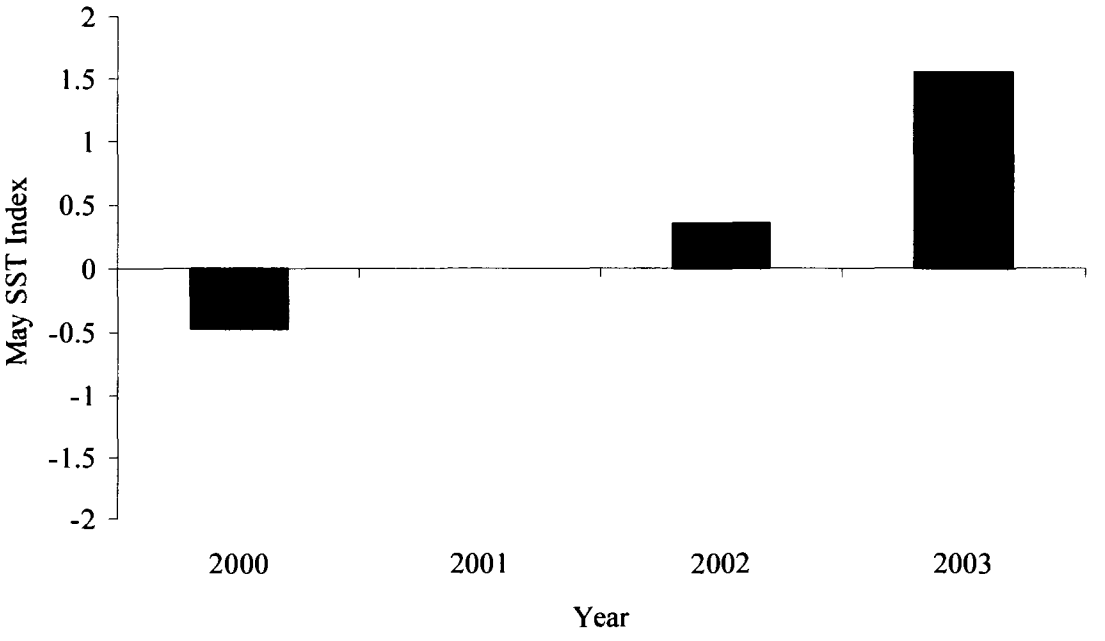

Figure 3.1. Index of sea surface temperatures (SSTs) during May 2000 to 2003 in the southeastern Bering Sea (http://www.beringclimate.noaa.gov). Mean May SSTs are averaged over the area 54°18' N to 60°0' N; 161°12' W to 172°30' W using data from the NCEP/NCAR project (Kalnay et al. 1996). The index values are the deviations from the mean May SST value (2.33° C) for the 1970 – 2000 period normalized by the S.D. (0.76° C).

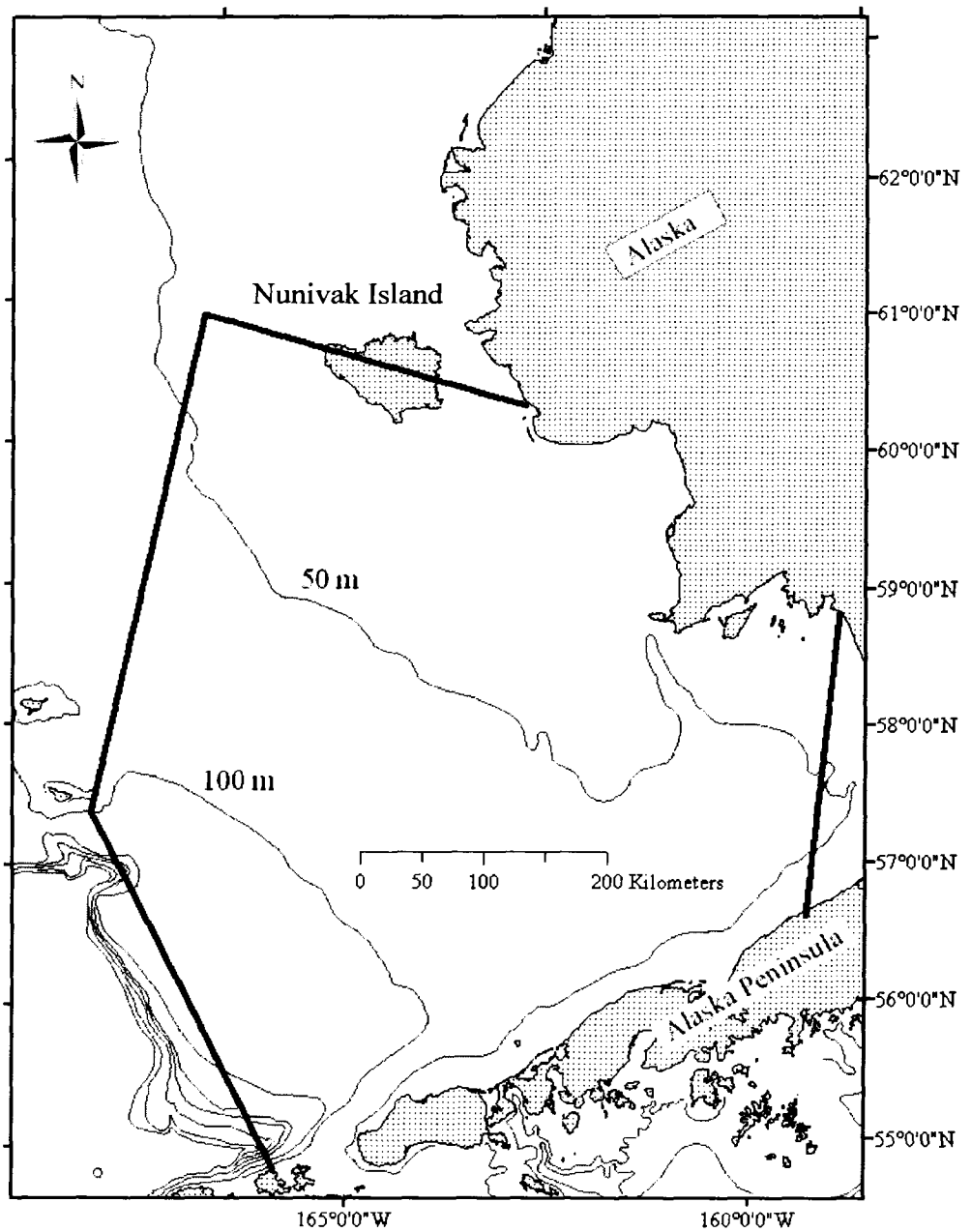

Figure 3.2. Area surveyed (within the dark line border) by the Ocean Carrying Capacity, Bering-Aleutian Salmon International Survey, August to September (2000 – 2003). Contours include the 50 m and 100 m bottom depth.

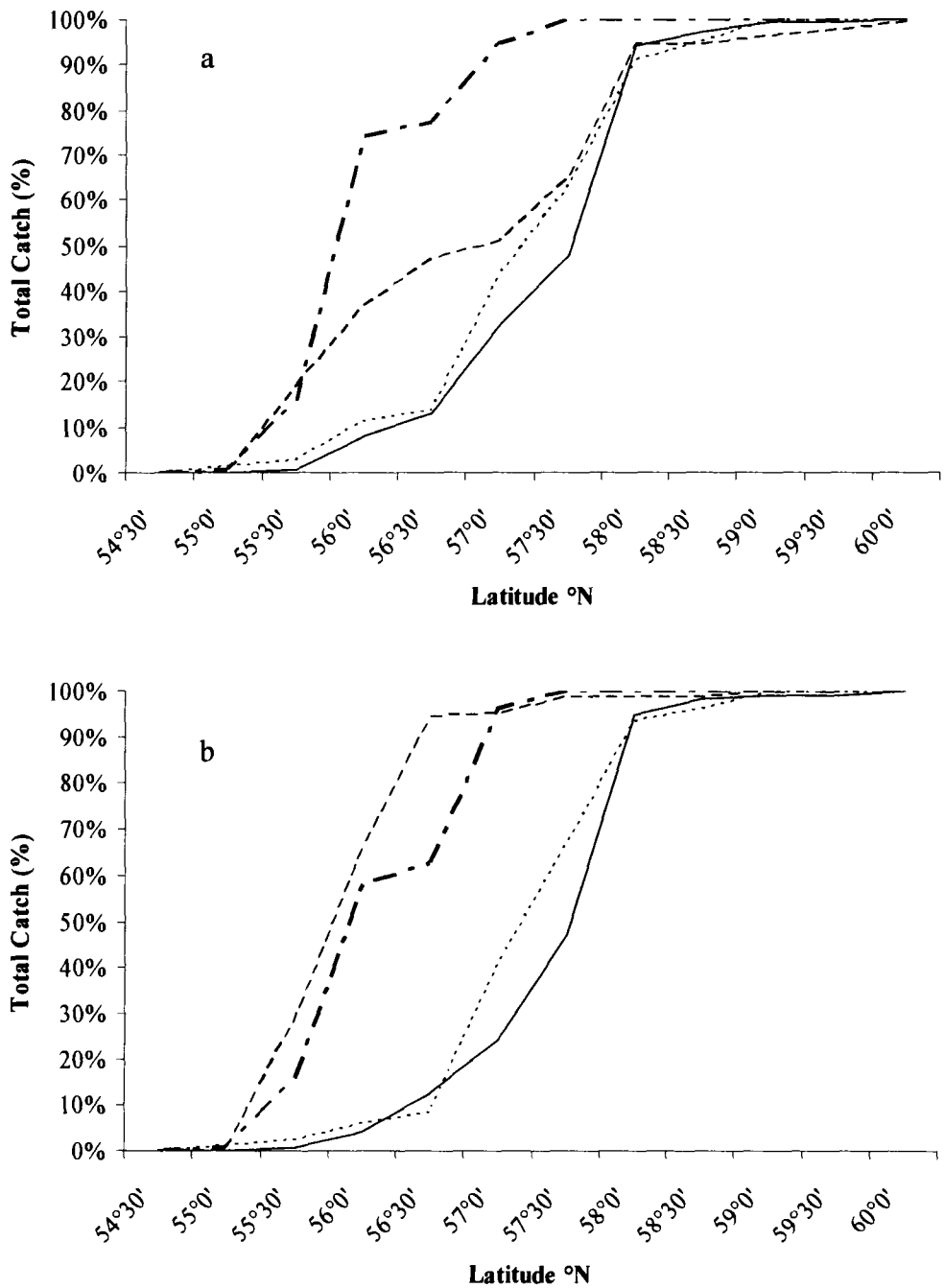

Figure 3.3. Cumulative percentage of total juvenile sockeye salmon catch south of latitudinal meridians in the area surveyed for (a) age 1.0 and (b) age 2.0 year sockeye salmon during August to September 2000 (----), 2001 (— – —), 2002 (——), 2003 (·····).

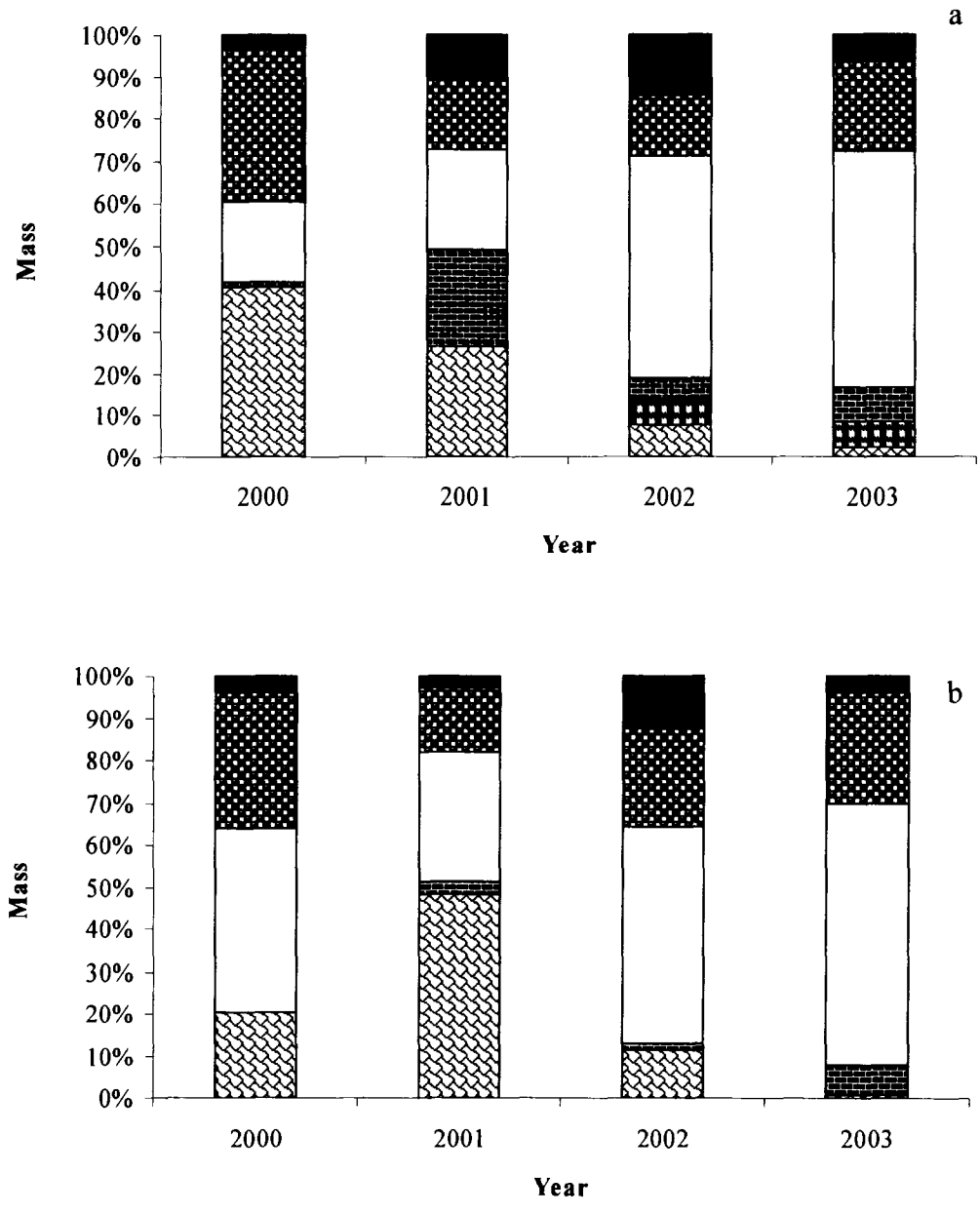

Figure 3.4. Juvenile sockeye salmon diets expressed as per cent by prey mass for age (a) 1.0 and (b) 2.0 year sockeye salmon collected along the eastern Bering Sea shelf during August to September 2000 – 2003. Diet data includes other zooplankton (dark bar; amphipods, arthropods, chaetognaths, copepods, *Limacina* sp. and mysids), other fishes (bubble bar, cottids, clupeids, *Sebastes* and pleuronectids), age 0 year pollock (clear bar), euphausiids (brick bar), Pacific herring (stippled; age 1.0 year sockeye salmon only) and Pacific sand lance (scales bar).

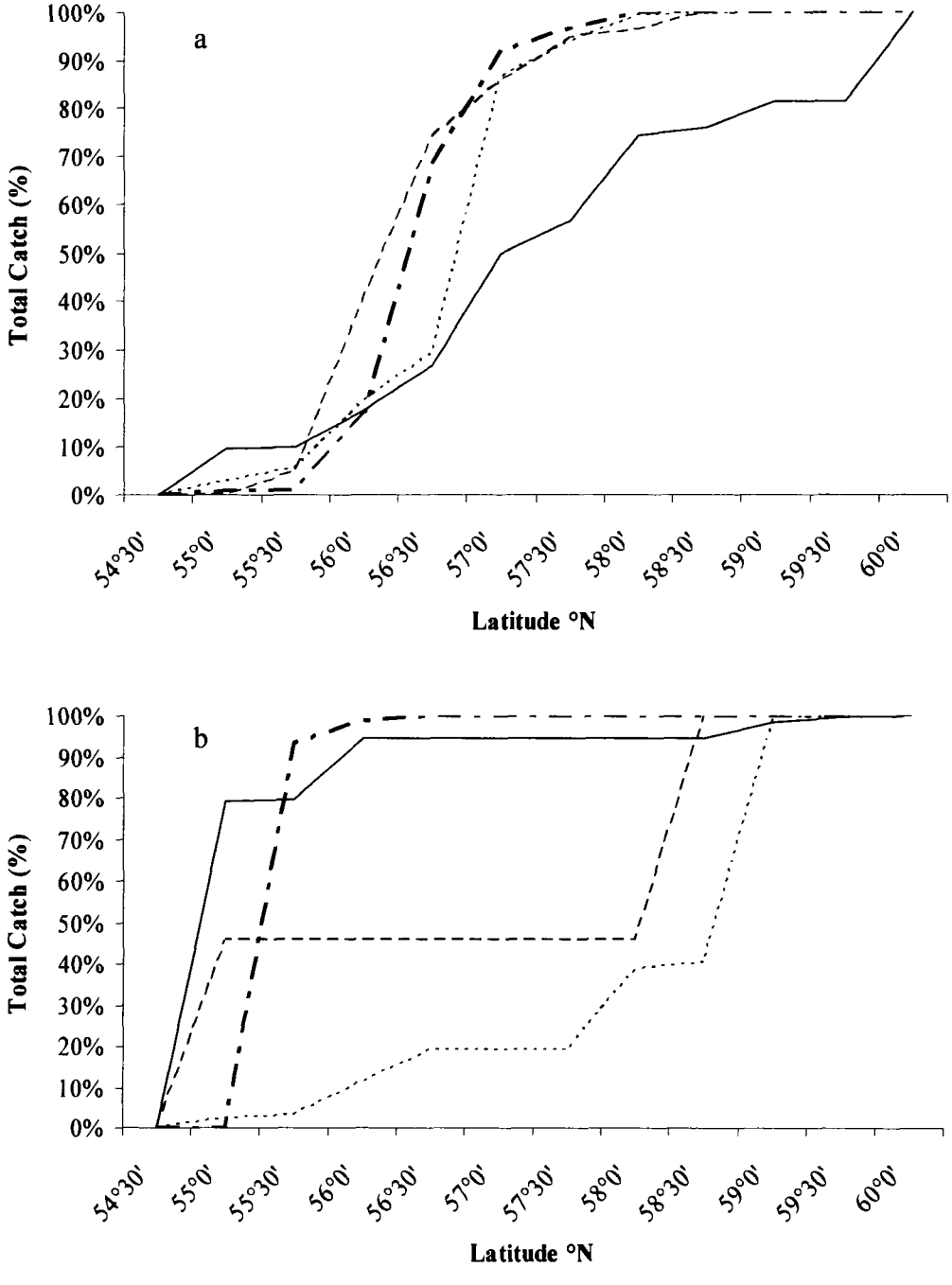

Figure 3.5. Cumulative percentage of the total catch south of latitudinal meridians in the area surveyed for (a) age 0 year pollock and (b) Pacific sand lance during August to September 2000 (----), 2001 (— – —), 2002 (——), 2003 (·····).

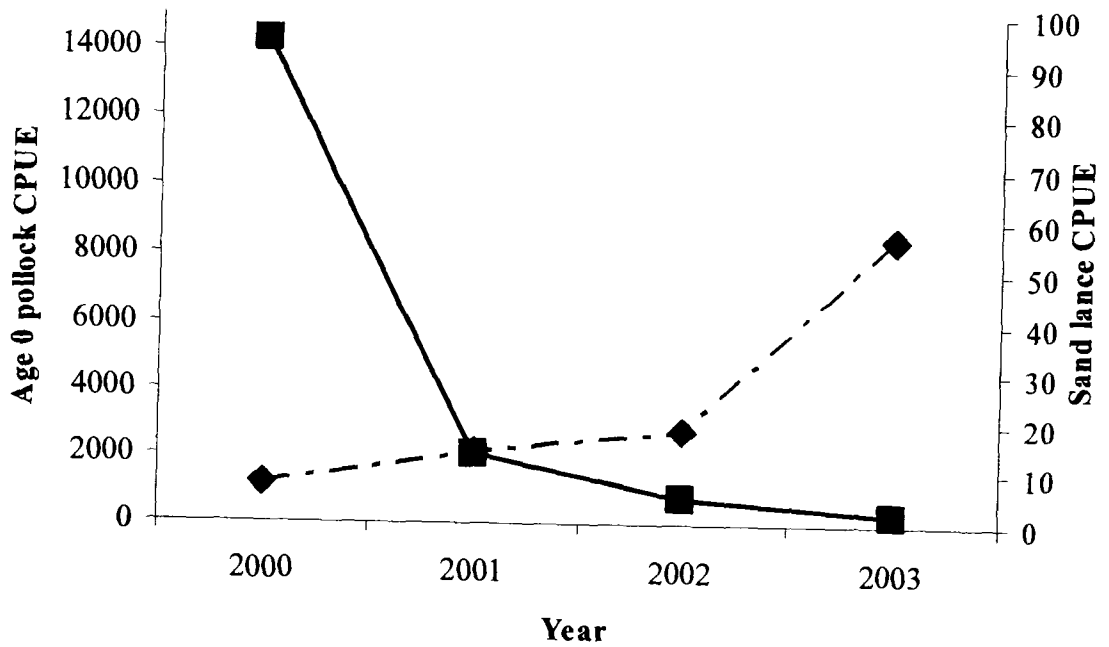

Figure 3.6. Relative abundance (catch per unit effort during a 30 minute trawl haul) of age 0 year pollock (— - —) and Pacific sand lance (——) during August to September 2000 to 2003.

TABLE 3.1. Mean ± S.E. fork length (L_F, mm), mass (M), and condition index (I_C) for age 1.0 and 2.0 years sockeye salmon collected over the eastern Bering Sea shelf during August – September, 2000 – 2003.

Age	Year	n	L_F	M (g)	I_C
1.0	2000	94	165·8±1·83	47·2±2·04	1·00±0·001
	2001	255	167·0±2·09	53·7±2·28	0·99±0·005
	2002	690	186·6±1·18	73·9±1·52	1·01±0·003
	2003	834	196·8±0·98	85·1±1·30	1·01±0·002
2.0	2000	95	182·7±2·13	63·2±2·11	0·98±0·008
	2001	204	193·2±2·68	83·0±3·31	0·97±0·005
	2002	371	211·3±2·15	113·5±3·21	1·01±0·003
	2003	1092	226·7±1·11	135·0±1·85	1·00±0·002

TABLE 3.2. Mean ± S.E. of the relative feeding index (I_{FR}) and the percent frequency of occurrence of fish with empty stomachs (%FE) for age 1.0 and 2.0 years sockeye salmon collected over the eastern Bering Sea shelf during August – September, 2000 – 2003.

Age	Year	*n*	I_{FR}	%FE
1.0	2000	72	-0·004±0·001	9·9
	2001	148	0·001±0·001	8·3
	2002	388	0·001±0·001	4·2
	2003	296	0·002±0·001	5·9
2.0	2000	65	-0·000±0·001	3·5
	2001	121	-0·000±0·001	4·4
	2002	226	-0·001±0·001	4·3
	2003	391	-0·001±0·001	5·9

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4 GROWTH RATE POTENTIAL OF JUVENILE SOCKEYE SALMON IN WARM AND COOL YEARS ON THE EASTERN BERING SEA SHELF[6]

4.1 ABSTRACT

Spatial and temporal variation in growth conditions for juvenile salmon may determine the survival of salmon after their first year at sea. To assess this aspect of habitat quality, a spatially explicit bioenergetics model was used to predict juvenile sockeye salmon *Oncorhynchus nerka* growth rate potential (GRP) on the eastern Bering Sea shelf during years with cool and warm spring sea surface temperatures (SSTs). Annual averages of juvenile sockeye salmon GRP were generally lower among years and regions with cool spring SSTs. In addition, juvenile sockeye salmon growth rate potential was generally higher in offshore than nearshore regions of the eastern Bering Sea shelf. The size and distribution (catch per unit effort) of juvenile sockeye salmon were not significantly ($P > 0.05$) related to GRP; this result was likely due to stock-specific dynamics (freshwater age structure) and annual variability in early marine growth prior to the August – September survey. Juvenile sockeye salmon prey densities were positively related to spring SST ($P < 0.05$). A sensitivity analysis indicated that juvenile sockeye salmon GRP was more sensitive to changes in observed sea surface temperature during years when prey densities were lower (2000 – 2002, and 2006). These

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results suggest the importance of bottom-up control on the eastern Bering Sea ecosystem for habitat quality of juvenile sockeye salmon in this region.

4.2 INTRODUCTION

Interannual differences in growth conditions in the ocean likely translate into annual variations in survival of juvenile, immature and maturing Pacific salmon *Oncorhynchus* spp. For juvenile salmonids, increased growth during the first year at sea confers a survival advantage with respect to predator avoidance (Parker 1968; Willette et al. 1999) and better condition of the fish during late fall and winter (Beamish and Mahnken 2001; Sogard 1997). Ocean conditions are believed to play a pivotal role in constraining early marine growth of juvenile salmon. For instance, sized-based natural mortality of juvenile coho salmon *O. kisutch* was hypothesized to be linked to available nutrients regulating the food supply and hence competition for food (Beamish and Mahnken 2001). Previous work on juvenile sockeye salmon *O. nerka* along the eastern Bering Sea shelf also suggested that smaller fish had lower survival (Farley et al. 2007b) and that size, condition and offshore distribution of these fish was connected to bottom-up control of the tropic structure on the eastern Bering Sea shelf (Farley et al. 2007a). Thus, linking salmon prey demand to prey supply and their dependence on habitat could provide insight into the complex dynamics between marine productivity and growth and survival of salmon.

Bioenergetics models that incorporate the spatial distribution of fish, their prey, and the physical conditions that affect foraging and growth are valuable for investigating the underlying basis for differences in habitat suitability (Nislow et al. 2000). Bioenergetics models stem from a species- and size-specific energy balance equation that describes the energy budget for a characteristic individual of a particular species (Kitchell et al. 1977). Individual species characteristics are generally expanded to the stock or population level by multiplying single fish dynamics by estimates of the population size and cohort mortality rate (Stewart et al. 1983; Hewett and Johnson 1992). Linking the stock or population bioenergetics models to temporally and spatially explicit habitat features (i.e. water temperature and potential prey) can lead to estimates of fish growth potential and/or habitat quality (Brandt et al. 1992; Mason et al. 1995; Luecke et al. 1999; Nislow et al. 2000).

Bioenergetics models that examine growth rate potential (GRP) for salmonids have been developed within streams (Nislow et al. 2000), large freshwater lakes (Goyke and Brandt 1993; Brandt et al. 2002; Roy et al. 2004), and marine ecosystems (Rand 2002). For juvenile salmonids during their first year in the ocean, energetics models have been used to investigate the effects of distribution or physiological and biological variables on salmon growth (Perry et al. 1996) and survival (Orsi et al. 2004). The results of this work have indicated that salmon in freshwater occupy habitats that support positive growth and that there are clear linkages to between prey biomass and salmonid recruitment success. For salmonids in the marine environment, GRP models have been

used to explain salmonid migratory behavior and describe regions where salmonids would experience higher or lower GRP in both space and time.

To develop an understanding of the link between juvenile sockeye salmon prey demand and supply, we estimated GRP over a 7-year period within four regions of the eastern Bering Sea shelf as a measure of habitat quality for juvenile sockeye salmon. Data on juvenile sockeye salmon and ocean conditions come from surveys conducted along the eastern Bering Sea shelf during mid August to early September 2000 to 2006. Our study is motivated by a leading hypothesis concerning ocean productivity on the eastern Bering Sea shelf suggests that spring ocean sea temperature affects prey availability to pelagic consumers; cool spring temperatures negatively affect available prey productivity and abundance (Hunt and Stabeno 2002), potentially impacting salmon growth and survival. The objectives were to determine if spring sea surface temperatures (SSTs) are associated with low or high juvenile sockeye salmon GRP and to examine whether GRP is a useful index for habitat quality for juvenile sockeye salmon on the eastern Bering Sea shelf. The bioenergetics model was used to test whether (1) GRP changed significantly among years and regions, (2) spring SSTs had an affect on regional variation in GRP, and (3) salmon size and densities were greater in regions with higher GRP. A sensitivity analysis was used to evaluate whether observed (August – September) SST or prey density had the strongest influence on model estimates of juvenile sockeye salmon GRP.

4.3 METHODS

4.3.1 *Study Area and Sampling Protocols*

Stations along the eastern Bering Sea shelf from longitudinal meridians 161°0' W to 166°0' W and from the Alaska Peninsula to 60°0' N at Nunivak Island were sampled during August – September 2000 – 2006 (Figure 4.1). For purposes of grouping sampling stations, oceanographic domains (coastal domain – well mixed, from shore to approximately 50 m depth, and middle domain – highly stratified, from 50 m to 100 m depth; see Kinder and Schumacher (1981) for description of domains) were split into smaller regions defined as "inner" and "outer" Bristol Bay; where inner Bristol Bay was defined as the area east of 163°30' W to 161°0' W and the outer region was defined as the area west of 163°30' W to 166°0' W (Figure 4.1). We defined the four areas as inner coastal (IC), inner middle (IM), outer coastal (OC), and outer middle (OM) regions.

Juvenile sockeye salmon were collected following methods described in Farley et al. (2005). Briefly, fish were collected using a mid-water rope trawl that is 198 m long, with a typical spread of 55 m horizontally and 15 m vertically. The trawl is constructed with hexagonal mesh in wings and body, and a 1.2-cm mesh liner in the codend. Trawl stations were located along longitudinal meridians spaced every 27.8 km during 2001 to 2003 and every 55.6 km during 2000, and 2004 to 2006. The survey area was fully sampled during all years except 2001, when sampling occurred only within the survey area from the Alaska Peninsula to 58°0' N because of rapidly declining catch per unit effort of juvenile sockeye salmon with distance to the north. The rope trawl was towed at 6.5 to 9.3 km/h with the head rope at or near surface. Trawl stations were sampled during

daylight hours (0730–2100, Alaska Daylight Savings Time) and all tows lasted 30 min and covered 2.8 to 4.6 km. A Seabird SBE-911 conductivity-temperature at depth (CTD) device was deployed at each station to measure the vertical profiles (from near bottom to surface) of ocean temperature. Ocean temperatures (°C) were collected during August to September 2000 to 2006 at 5 m depth (CTD; observed sea surface temperature (OSST)) at each station were used for bioenergetics modeling. At each trawl station, juvenile sockeye salmon were selected at random (maximum 50) and standard biological attributes, including fork length (nearest mm) and body weight (nearest g) of juvenile sockeye salmon were measured onboard.

4.3.2 *Bioenergetics Model*

The GRP of juvenile sockeye salmon over the eastern Bering Sea shelf was estimated using the bioenergetics model developed by Ware (1978) as modified by Trudel and Welch (2005). This model was parameterized for sockeye salmon and accounts for optimal cruising speed:

$$G_{i,s} = \tau \cdot I_{i,s} - (SMR_{i,s} + ACT_{i,s}) \quad (1)$$

where $G_{i,s}$ is the GRP (cal/s) for juvenile sockeye salmon during year i at station s, τ is the proportion of food that can be metabolized (Trudel and Rasmussen 2006), $I_{i,s}$ is the feeding rate (cal/s), $SMR_{i,s}$ and $ACT_{i,s}$ are respectively the standard metabolic rate (cal/s) and activity costs (cal/s).

Feeding rate is likely a function of prey density (Ware 1978). Unfortunately, no empirical studies have been performed to date to examine the relationship between salmon feeding rate and prey density in natural conditions (Walters et al. 1978), probably

due to the difficulty in estimating *in situ* food consumption rates. Thus, the relationship between salmon feeding rate and prey density was assumed to be described by a type II functional response (Ware 1978):

$$I_{i,s} = \frac{\rho_{i,s}\gamma_{i,j}U_{i,s}}{1+\rho_{i,s}\gamma_{i,j}h_{i,j}U_{i,s}} \tag{2}$$

where ρ is prey density (cal/cm^3) during year i and station s, γ is the cross sectional area of the reactive field (cm^2) during year i and region j, U is the optimum swimming speed (cm/s), and h is handling time (s/cal). Equation (2) reaches an asymptote at:

$$I_{\max} = \lim_{\rho\to\infty}\frac{\rho\cdot\gamma\cdot U}{1+\rho\cdot\gamma\cdot h\cdot U} = \frac{1}{h} \tag{3}$$

where I_{max} is the maximum feeding rate (cal/s). We used the equation derived by Beauchamp et al. (1989) for the maximum feeding rate (g/d) for sockeye salmon to parameterize the handling time:

$$I_{\max} = ED_p \cdot CA \cdot \overline{W}_{i,j}^{1-CB} \cdot f(T) \tag{4}$$

where ED_p is prey caloric content (cal/g_{wet}), W is sockeye salmon weight (g), CA and CB are respectively the weight coefficient and exponent for maximum feeding rate, and $f(T)$ is the Thornton and Lessem (1978) temperature dependence function for cool- and cold-water fish species (see Table 1 for definition and parameters). Thus, we substituted $\frac{1}{h}$ for $I_{\max}$ in equation (4):

$$h = \alpha_4 \overline{W}_{i,j}^{CB-1} \tag{5}$$

where,

$$\alpha_4 = \frac{1}{ED_p \cdot CA \cdot f(T)} \tag{6}$$

The energetic costs associated with the standard metabolic rates and activity costs of juvenile sockeye salmon were modeled using the empirical models derived by Trudel and Welch (2005). Specifically, standard metabolic rates were modeled as a function of weight and water temperature (°C):

$$SMR_{i,s} = \alpha_1 \overline{W}_{i,j}^{\beta} e^{\varphi T_{i,s}} \tag{7}$$

where α_1, β, and φ are regression coefficients (Table 1). Activity costs were modeled as a function of weight and swimming speed:

$$ACT_{i,s} = \alpha_0 \overline{W}_{i,j}^{\delta} U_{i,s}^{\lambda} \tag{8}$$

where α_0, δ, and λ are regression coefficients (Table 1). We used the optimal cruising speed model derived by Trudel and Welch (2005) to estimate the swimming speed of juvenile sockeye salmon (Table 1).

4.3.3 *Prey Abundance*

Gut contents from subsamples of juvenile sockeye salmon at each trawl station were analyzed to characterize prey consumption (Farley et al. 2007a; Farley et al. in review). Prey analyses determined that fish, including age 0 walleye pollock (*Theragra chalcogramma*) and Pacific sand lance (*Ammodytes hexapterus*) dominated (60% to 70%) the percent wet weight of stomach contents. The other major prey item was Euphausiidae species (approximately 20% wet weight during 2006 only); however, biomass estimates for these species were not available, thus only age 0 pollock and sand lance were considered the primary "prey" for bioenergetics models. The typical size

ranges of age 0 pollock and sand lance in the diets of juvenile sockeye salmon were between 28 to 67 mm and 55 to 80 mm, respectively (Farley et al. 2007a). Age 0 pollock were measured as total length and sand lance were measured as fork length, and reported in this manner throughout the paper.

Prey energy density (cal/cm^3) at each station was determined as:

$$\rho_{i,s} = \sum_{p=1}^{2} \frac{N_{i,s,p} \cdot \theta \cdot ED_p \cdot \overline{W}_p}{\phi \cdot V_{i,s}} \tag{9}$$

where $N_{i,s,p}$ is the number of prey (p = age 0 pollock or sand lance) caught at each station, θ is the proportion of prey items captured in trawls that fell within the size range that juvenile sockeye salmon fed upon (dimensionless), ED_p is defined above, $\overline{W}_p$ is the average weight (g) for each prey item, ϕ is the catchability coefficient (dimensionless), and $V_{i,s}$ is the volume sampled at each station (cm^3). Volume sampled at each station was estimated by multiplying the distance trawled (cm) by the vertical (cm) and horizontal (cm) spread of the net opening.

The catchability coefficient of age 0 pollock was determined by comparing catches during the Bering-Aleutian Salmon International Surveys (BASIS) research cruises to hydroacoustic survey estimates (Swartzman 2004). The BASIS research cruises cover a large area of the eastern Bering Sea shelf, and age 0 pollock and sand lance are typically captured (see Farley et al. 2007a). The average density of age 0 pollock in BASIS surveys conducted along the eastern Bering Sea shelf during 2000 to 2006 was 0.003/m^3 compared to 0.191/m^3 during acoustic surveys near the Pribilof Islands during August 1996 - 1997 (Swartzman 2004). These differences in number of

age 0 pollock per m^3 could be due to interannual variability (1996 and 1997 vs 2000 to 2006), different area surveyed (transects offshore of the Pribilof Islands vs. stations covering a much broader area of the eastern Bering Sea shelf), gear type (acoustic measurements designed to target age 0 pollock vs pelagic trawl designed to capture small salmon), and depth (acoustic estimates were from near surface to near bottom depths where as the trawl fished from near surface to approximately 15 m depth).

Because the abundance of age 0 pollock sampled along transects in the vicinity of the BASIS surveys was similar to that near the Pribilof Islands during 1999 (Coyle and Pinchuk 2002), area effects were discounted. In addition, average pollock recruitment to age 1 from acoustic surveys conducted during 1997 and 1998 was similar to that for 2001 to 2005 (23,599.2 million vs. 18,664.9 million; Jim Ianelli, personal communication). The vertical distribution of age 0 pollock during summer can range from surface to bottom on the eastern Bering Sea shelf (see Coyle and Pinchuk 2002). Studies on vertical distribution of age 0 pollock at oceanic fronts near the Pribilof Islands (Schabetsberger et al. 2000) suggest that highest densities of these fish occur below 30 m during the day, however dense aggregated fish shoals can be found above 20 m depth during day. In addition, the highest densities of age 0 pollock occur above 20 m during night, indicating that these fish vertically migrate to the near surface waters during night (Schabetsberger et al. 2000).

Juvenile sockeye salmon feed during daylight hours and data from our survey indicate that their stomachs are generally fullest during afternoon and evening hours. Due to variability in vertical distribution of age 0 pollock for both day and night, we

chose 25% as a conservative estimate of the percentage of age 0 pollock available to juvenile salmon in the top 15 m of the water column during daylight hours. So, a catchability coefficient of 0.063 for the BASIS pelagic trawl was determined by dividing the average number of age 0 pollock per m^3 caught during BASIS cruises by the average number of age 0 pollock per m^3 determined by Swartzman (2004) multiplied by 0.25, the fraction of age 0 pollock available in the upper 15 m of the water column (i.e., 0.003/(0.191*0.25)). Similar comparisons for juvenile sand lance could not be made due to lack of published abundance estimates on the eastern Bering Sea shelf; the catchability coefficient for this prey item was assumed to be the same as age 0 pollock.

A comparison between lengths for age 0 pollock and sand lance captured in the trawl net and in gut contents of juvenile sockeye salmon indicated approximately 68% of age 0 pollock and 59% of the sand lance caught in the trawl were within the size range that juvenile sockeye salmon fed upon (typical size range for age 0 pollock and sand lance in the trawl samples was between 45 and 95 mm and 77 to 150 mm, respectively; Farley et al. 2007a). The average weight of these prey was 1.7 g for age 0 pollock and 1.2 g for sand lance. Laboratory analyses of subsamples of age 0 pollock taken during the 2005 survey indicated that the average caloric content was 4,424 cal/g_{dry}; caloric content for Pacific sand lance (4,209 cal/g_{dry}) was obtained from Robards et al. (1999). The estimates of catchability, proportion of prey items, caloric content, and weight were held constant for each station, among years.

Growth rate potential (cal/s) was converted to cal/d by multiplying $I_{i,s}$ by the number of seconds in a 15 hour day (estimated time juvenile sockeye salmon spend

feeding per day during August and September) and by multiplying $SMR_{i,s}$ and $ACT_{i,s}$ by the number of seconds in a 24 hour day.

Estimated daily GRP (cal/d) at each station s was then expressed as a percentage of body weight (% body weight/d) for each station s by dividing estimated daily GRP (cal/d) by the total energy per fish (cal) as (Perry et al. 1996):

$$\overline{E}_{i,s} = ED_f \cdot \overline{W}_{i,j} \tag{10}$$

where $\overline{E}_{i,s}$ is the average total energy per fish (cal) during year i and at station s, ED_f is the caloric content in juvenile sockeye salmon (cal/g_{wet}), and $\overline{W}_{i,j}$ is the average weight (g) of juvenile sockeye salmon during year i and in region j. Annual averages of juvenile sockeye salmon weight within a region were used as opposed to average weight of these fish at each station because there were stations within a region where no juvenile sockeye salmon were caught. The caloric content of juvenile sockeye salmon was determined from subsamples of the juvenile sockeye salmon caught during the 2002 to 2005 surveys using bomb calorimetry and averaged 5,111 cal/g_{dry}. There was no significant difference in average caloric content of juvenile sockeye salmon among years; (ANOVA- Fixed effect, $F = 5.3$, $P = 0.08$); caloric content of juvenile sockeye salmon was not available for 2000, 2001, or 2006. The units (cal/g_{dry}) were converted to (cal/g_{wet}) by multiplying 5,111 cal/g_{dry} by 23% (W g_{dry}/ W g_{wet}), the average value obtained from the subsample (2002 to 2005) of juvenile sockeye salmon dried for the bomb calorimetry process. These estimates of growth (% body weight/d) were considered to be juvenile sockeye salmon GRP on the eastern Bering Sea shelf and were the primary statistic used in subsequent models.

4.3.4 *Spring SSTs*

Spring SSTs during May 2000 to 2006 in the southeastern Bering Sea are shown in Figure 4.2. Mean May SSTs were averaged over 54°18' N to 60°0' N, 161°12' W to 172°30' W (data from www.beringclimate.noaa.gov). Index values were calculated as the deviations from the mean May SST value (2.33° C) for the 1970 – 2000 period divided by the standard deviation (0.76° C). Years with cool SSTs were defined as those years when the index values of SSTs were at or below 0 (2000, 2001, and 2006); years with warm SSTs were defined as those years when the index values of SSTs were above 0° C (2002 to 2005).

4.3.5 *Model Applications*

H1:GRP differs significantly among years and regions and *H2:GRP differs significantly among regions that experienced warm versus cool spring SSTs* –These hypotheses were tested using two-way analysis of variance (ANOVA-Fixed Effect) with S-plus software (Insightful, 2001). For H1, year (2000 to 2006) and region (IC, IM, OC, and OM) were the categorical variables and GRP was the dependent variable. For H2, spring SSTs (cool and warm) and region (IC, IM, OC, and OM) were the categorical variables and GRP was the dependent variable. If a significant difference ($P < 0.05$) occurred, a Sidak multiple comparison test was used to calculate the 95% ($\alpha = 0.05, 0.01, 0.001$) confidence intervals for all pairwise differences between the dependent variable means (Insightful, 2001). The level of significance between the pairwise differences was determined by examining those confidence intervals that excluded zero for the three values of α.

H3:Regional averages of GRP *are positively related to regional averages of juvenile sockeye salmon size and CPUE* and *H4: Annual averages of GRP are positively related to annual indices of spring SSTs* – Regression analysis was used to examine the relationship between annual averages of regional GRP and annual averages of regional fork length (cm) and catch per unit effort (CPUE – defined as the number of juvenile salmon caught during a 30 minute trawl haul, averaged within a region). Regression analysis was also used to examine the relationship between annual averages of juvenile sockeye salmon GRP and spring SSTs. The relationship between observed prey density and spring SSTs was also examined using regression analysis.

4.3.6 *Sensitivity Analysis*

The sensitivity of the model's estimates of GRP was estimated by varying OSST and prey density (no./cm^3) by ± 20% at each station during year *i*. The objective was to examine to what extent sea surface temperatures affect GRP for juvenile sockeye salmon as opposed to observed prey abundance. The variability of ± 20% was chosen because this difference was close to the difference in the OSST between years with cool (2000, 2001, and 2006) and warm (2002 to 2005) spring SSTs (Figure 4.2). For each analysis, one of the inputs was held constant while adjusting the other by ± 20%. A sensitivity value of 0.0 or 1.0 means (for example) that a 20% increase in OSST or prey abundance resulted in no increase or a 20% increase in estimated GRP for juvenile sockeye salmon.

4.4 RESULTS

4.4.1 *Hypothesis Tests*

H1. – Juvenile sockeye salmon GRP differed significantly among years (ANOVA; $f_{[6,344]} = 12.68$, $P < 0.001$; Table 4.2) and regions (ANOVA; $f_{[3,344]} = 6.69$, $P < 0.001$). The interaction between region and year was also significant (ANOVA; $f_{[18,344]} = 2.03$, $P = 0.008$; Table 4.3). In general, mean annual GRP was negative for all years except 2004. The pairwise comparison among years indicated that average GRP was significantly higher ($P < 0.001$) during 2004 than all other years. In general, GRP was negative for all regions except 2004 and within the IM and during 2003 and the OM region during 2005 (Table 4.3). The pairwise comparison within year indicated that GRP in the IM region was significantly higher than GRP in the OC ($P < 0.05$), IC ($P < 0.01$), and OM ($P < 0.01$) regions during 2004. In addition, GRP in the OM region was significantly higher than GRP in the OC ($P < 0.05$) and IC ($P < 0.01$) regions during 2005. The pairwise comparison among years indicated that GRP in the IM region was significantly higher during 2004 than during 2000 ($P < 0.01$) and 2005 ($P < 0.01$) as well as significantly higher ($P < 0.001$) than 2001, 2002, 2003, and 2006. The GRP in the OC region was significantly higher ($P < 0.05$) during 2004 than during 2000, 2002, and 2003. The GRP in the OM region was significantly higher during 2004 ($P < 0.05$) than 2001, as well as significantly higher during 2005 than 2000 ($P < 0.05$), 2001 ($P < 0.001$), 2002 ($P < 0.05$) and 2006 ($P < 0.05$).

H2. – Juvenile sockeye salmon GRP differed significantly among regions (ANOVA; $f_{[3,364]} = 6.16$, $P < 0.001$) and between cool and warm spring SSTs (ANOVA; $f_{[1,364]} = 21.72$, $P < 0.001$; Figure 4.3). The interaction between region and spring SSTs was not significant (ANOVA; $f_{[3,364]} = 2.29$, $P = 0.08$; Figure 4.3). The pairwise

comparison among regions indicated that GRP was significantly higher during warm than cool spring SSTs in the IM ($P < 0.01$) and OM ($P < 0.001$) regions. During warm spring SSTs, GRP in the IM region was significantly higher than in the OC ($P < 0.001$) and IC ($P < 0.01$) regions.

H3. – Regional averages of juvenile sockeye salmon GRP were not significantly related to length ($F = 0.01$, $P = 0.93$; Figure 4.4) or CPUE ($F = 1.00$, $P = 0.33$; Figure 4.5).

H4. –Nearly significant, positive relationships between annual averages of juvenile sockeye salmon GRP and indices of May SST ($F = 5.78$, $P = 0.06$; Figure 4.6) were found. In addition, a significant, positive relationship between observed prey density and May SST was found ($F = 7.96$; $P = 0.04$; Figure 4.7).

4.4.2 *Sensitivity Analysis*

In general adjusting prey density and OSST by 20% lead to less than 20% change in GRP during all years except 2003 and 2005 (Table 4.4). With the exception of 2004, a 20% change in OSST from observed values resulted in the largest percent differences in GRP during years with warm springs (2002, 2003, and 2005). In all years, increasing OSST lead to a decline in juvenile sockeye salmon GRP, whereas increasing prey density lead to positive increases in juvenile sockeye salmon GRP.

4.5 DISCUSSION

Our findings suggest a possible connection between GRP of juvenile sockeye salmon during late summer, early fall and spring SSTs along the eastern Bering Sea shelf.

On average, salmon GRP was lower during years with cool rather than warm spring SSTs and that salmon GRP was highest in offshore regions (IM and OM) during years with warm spring SSTs (supporting H1 and H2). These results are in line with previous findings that larger juvenile sockeye salmon were found during years with warm spring SSTs, where larger size after the first summer at sea was speculated to have been the result of increased productivity on the eastern Bering Sea shelf leading to higher prey densities and faster growth rates for juvenile sockeye salmon (Farley et al. 2007a).

Reinforcing our model predictions, we found a positive, significant relationship between annual averages of observed prey density and spring SSTs (H4). There are several relationships that appear to be important in governing production on the eastern Bering Sea shelf (Hunt and Stabeno 2002). The onset of spring net primary production on the eastern Bering Sea shelf is linked to the timing and duration of ice cover and winter winds. According the Hunt and Stabeno's (2002) OCH, during years with extensive ice cover, a delay in ice melt stratifies the upper water column late enough in spring such that incident solar radiation is sufficiently high to cause an early spring phytoplankton bloom. However, because the ocean is too cold for zooplankton reproduction, most of the primary productivity falls ungrazed to the seafloor. During years of little sea ice, ice-edge stratification of the water column is weaker and occurs too early in the season before solar radiation is strong enough to support a phytoplankton bloom. So, the phytoplankton bloom occurs later in spring after the water column has become thermally stratified. Higher mesozooplankton production occurs during years with warm spring ocean temperatures than in years when the bloom occurs in cold water

at the ice edge, because warmer temperatures promote a tighter coupling between zooplankton and phytoplankton.

The size of juvenile sockeye salmon was expected to be significant and positively related to GRP, but instead regional averages of juvenile sockeye salmon length were not significantly related with spatial distributions of GRP (not supporting H3). Juvenile sockeye salmon from Bristol Bay spend one or more years in freshwater; freshwater age 2.0 fish are larger than freshwater age 1.0 fish when they leave lakes and enter the marine environment (Burgner 1991). In addition, there are stock-specific differences in smolt size among the Bristol Bay lake systems (Burgner 1991) and early marine growth rates of juvenile sockeye salmon prior to the late summer survey. For example, Farley et al. (2007a) proposed higher growth rate as the most plausible explanation for changes in observed smolt and juvenile sockeye salmon size during 2002. In support of the hypothesis, previous research indicated size distributions of juvenile sockeye salmon increased with distance from river mouth and displayed a bell shaped curve offshore from the southern shoreline (Alaska Peninsula), with the largest fish distributed within middle Bristol Bay (i.e. IM, OM) and the smallest fish along the southern and northern shorelines (i.e. IC, OC; Farley et al. 2005). It is likely that annual variability in the proportion of freshwater age, stock structure, and early marine growth prior to the late summer, early fall survey, confound these results, making it difficult to relate juvenile sockeye salmon size and GRP taken at a finite time period on the eastern Bering Sea shelf.

In addition, juvenile sockeye salmon CPUE was positively associated with GRP, but the relationship was not significant (not supporting H3). Upon entering marine waters of the eastern Bering Sea, juvenile salmon generally remain nearshore (Straty 1974, Martin et al. 1986). As salmon grow, they move offshore. Two differing seaward migration models are believed to exist for juvenile Bristol Bay sockeye salmon; in some years juvenile sockeye salmon migrate along the coastal waters of the eastern Bering Sea near the Alaska Peninsula, and in other years their migration is farther offshore (Farley et al. 2005). Farley et al. (2007a) speculated that the location of the seaward migration pathway is related to ocean temperatures during spring with a nearshore migration pathway during cool years and an offshore migration pathway during warm years. In general, GRP among regions of the eastern Bering Sea was higher during years with warm spring SSTs. In addition, GRP was higher offshore during years with cool spring SSTs. While spatial distributions of CPUE and GRP of juvenile sockeye salmon are not significantly related, evidence indicates that a nearshore distribution during years with cool spring SSTs places juvenile sockeye salmon in regions with lower GRP and offers some explanation as to why years with cool spring SSTs are associated with smaller size, lower condition, and reduced marine survival for juvenile sockeye salmon (Farley et al. 2007a, Farley et al. 2007b).

Our goal was to use growth rate potential as an indicator of habitat quality during years with cool and warm spring SSTs, rather than to provide precise quantitative estimates of growth rate for juvenile sockeye salmon. For instance, juvenile sockeye salmon GRP was negative during all years except 2004 indicating that these salmon are

loosing rather than gaining weight in 6 of the 7 years studied. The annual estimates of juvenile sockeye salmon average GRP varied from -0.89% to 0.67% (% body weight per day). Juvenile salmon growth rate is size dependent, daily growth rate decreases as the fish get larger (Brett 1974). The average weight (g) of all juvenile sockeye salmon collected along the eastern Bering Sea shelf over the 7 year period was 74.0g; the growth rate of "wild" juvenile sockeye salmon raised experimentally in salt water tanks and fed until satiated twice a day was approximates 1.01% per day for 110g fish (Brett 1974). Thus, our estimates may not be out of line with experimental estimates of juvenile sockeye salmon daily growth rate because our juvenile sockeye salmon were collected in the wild under varying OSSTs and prey densities.

Conversely, previous results indicated that these same juvenile sockeye salmon had full stomachs, were larger, and in better condition during 2002 and 2003 (years with negative GRP) compared to previous years (2000 and 2001; Farley et al. 2007a). Bioenergetics models are particularly sensitive to changes in energy density, composition of stomach contents, and biomass of potential prey (Beauchamp et al. 1989). Our estimates of available prey biomass were generated using a number of assumptions that could potentially lead to a bias of under/over estimating the number of dominant prey (age-0 pollock and Pacific sand lance) available to juvenile sockeye salmon on the eastern Bering Sea shelf. In addition, we chose to generate abundance estimates of the dominant prey items even though other prey items made up to 30% of the stomach contents for juvenile sockeye salmon during some years. Thus, the most plausible explanation for negative GRP is that our estimates of prey biomass were biased low.

However, because we maintained these assumptions for all years, comparisons of the relative differences in juvenile salmon GRP would likely provide robust estimates of changes in juvenile sockeye salmon GRP among the years examined.

The bioenergetics model indicated that juvenile sockeye salmon GRP was more sensitive to changes in OSST during years when prey densities were lower (2000 – 2002, and 2006). In addition, increasing OSST by 20% in the model resulted in decreasing juvenile sockeye salmon GRP from 6% to 96%, with the largest percent decrease occurring during years when OSSTs were warmest (2003 and 2005; Figure 4.2). These results may herald negative consequences for juvenile sockeye salmon on the eastern Bering Sea shelf in the future. It is generally agreed that the climate in the Arctic and Bering Sea is warming (Stabeno et al. 2001). Although warm spring SSTs have been hypothesized to increase pelagic productivity on the eastern Bering Sea shelf (Hunt and Stabeno 2002), physical changes in the Bering Sea under a global warming scenario are expected to reduce the supply of nutrients to the shelf region (US GLOBEC 1996). Thus, productivity on the eastern Bering Sea shelf could be negatively impacted, in turn, lowering abundance of potential prey for juvenile sockeye salmon. Increasing SSTs and lower abundance of potential prey would negatively impact juvenile sockeye salmon GRP, potentially leading to smaller size and lower marine survival for juvenile Bristol Bay sockeye salmon.

Our study provides evidence that energetic limitation influences habitat quality on the eastern Bering Sea shelf for juvenile sockeye salmon during years with cool spring SSTs. Abundance of the primary prey for juvenile sockeye salmon is higher during years

with warm spring SSTs, and the abundant prey was likely due to increased primary and secondary productivity in the pelagic ecosystem during these years (Hunt and Stabeno 2002). In addition, warmer spring temperatures lead to earlier lake-ice break-up and, in turn, juvenile sockeye salmon smolt generally begin their seaward migration within days of ice break-up (Burgner 1991). Thus, it appears that juvenile sockeye salmon gain a survival advantage during years with warmer spring temperatures due to the extended growing season and increased productivity (bottom-up control) on the eastern Bering Sea shelf. As such, this work is an instructive case study and is a framework for future research on juvenile salmon energetics in large marine ecosystems.

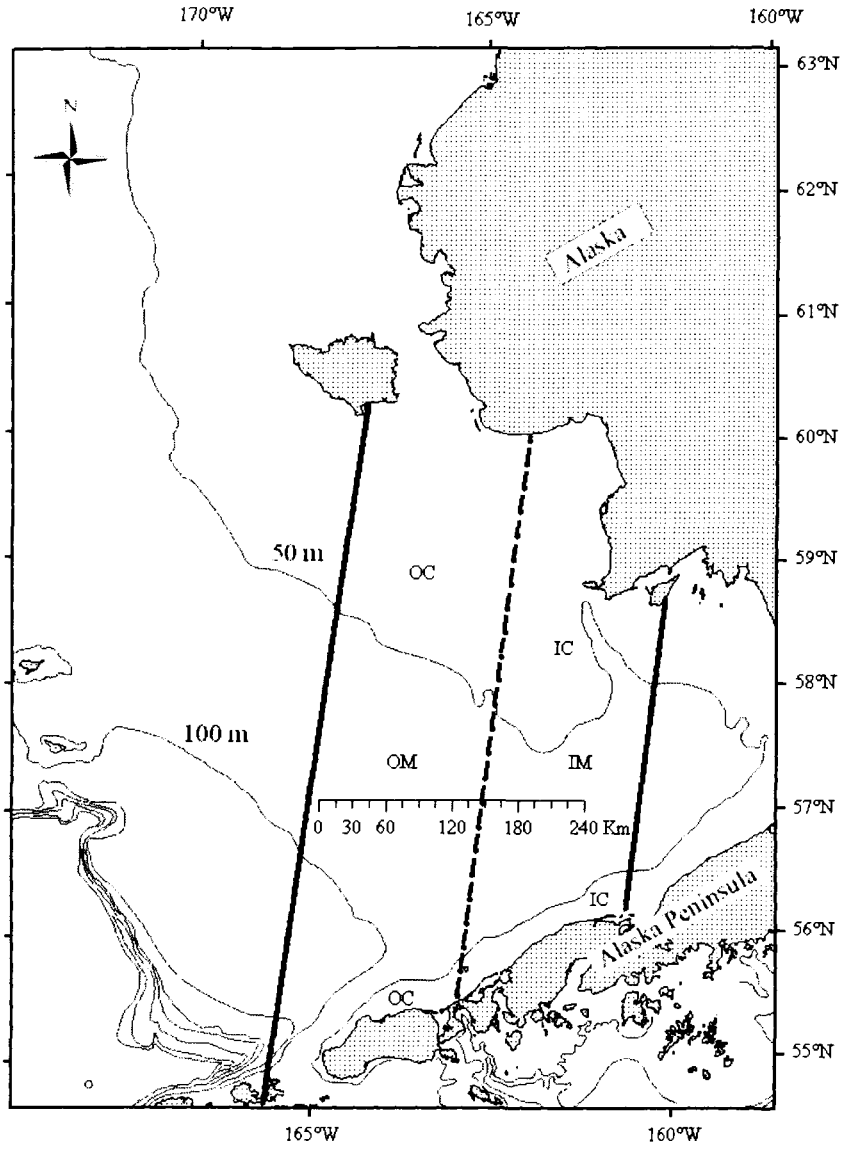

Figure 4.1. Areas surveyed (between 161°W to 166°W; dark lines. Dashed line at 163.5°W) for juvenile sockeye salmon during August – September 2000 to 2006 Ocean Carrying Capacity, BASIS research cruises. The regions include inner coastal (IC; area west of 161°W to 163.5°W from coastal margins to the 50 m contour), inner middle (IM; area west of 161°W to 163.5°W and bordered by 50 m contour), outer coastal (OC; area west of 163.5°W to 166°W from coastal margins to the 50 m contour), and outer middle (OM; area west of 163.5°W to 166°W and bordered by 50 m contour).

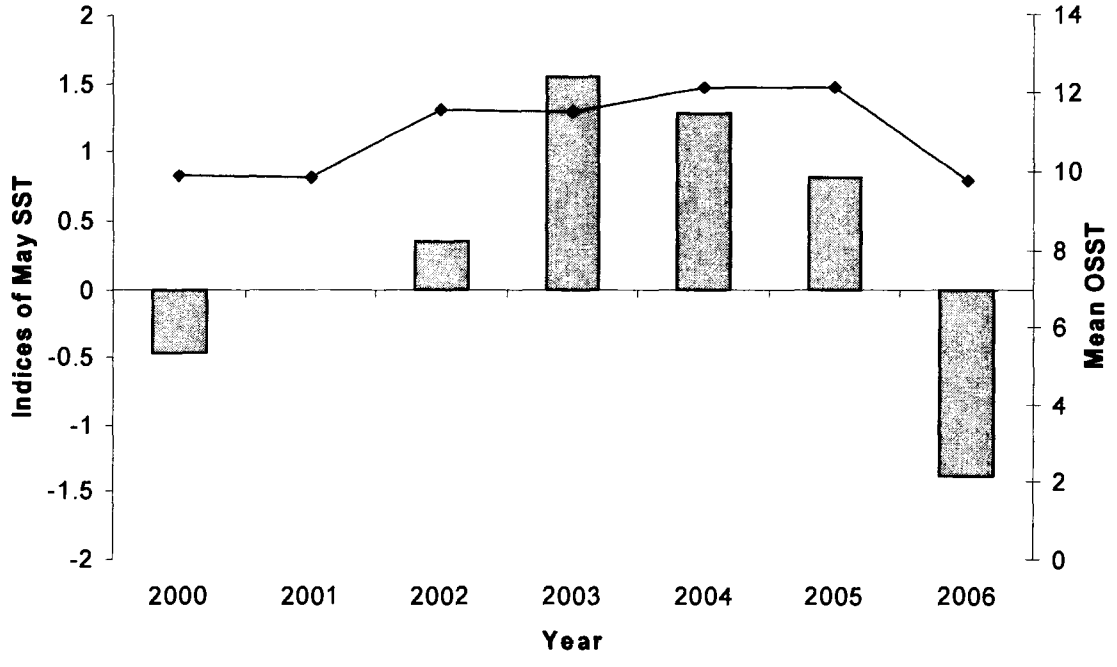

Figure 4.2. Indices of sea surface temperatures (bar, SSTs,°C) during May 2000 to 2006 in the southeastern Bering Sea (data obtained from http://www.beringclimate.noaa.gov) and annual averages (line) of observed SSTs (OSST, °C) collected during August to early September surveys. Mean May SSTs are averaged over the area 54°18' N to 60°0' N, 161°12' W to 172°30' W using data from the NCEP/NCAR reanalysis project (Kalnay et al. 1996). The index values are the deviations from the mean May SST value (2·33° C) for the 1970 – 2000 period normalized by the standard deviation (0·76° C). Mean OSSTs (°C) are the averages of observed SSTs at 5 m depth taken at stations conducted within the survey area of Figure 1.

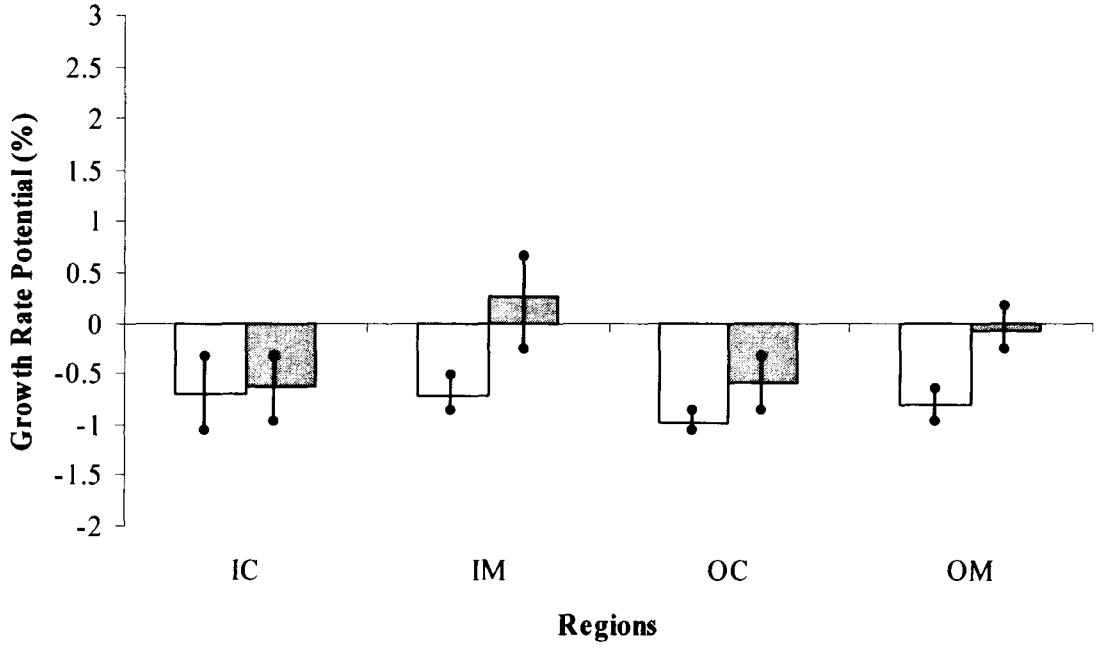

Figure 4.3. Regional averages (±SE, block dots) of growth rate potential (% body weight per day) of juvenile sockeye salmon during years with cool (open bars) and warm (shaded bars) spring SSTs. Regional averages were estimated by pooling stations collected during years with cool (2000, 2001, and 2006) and warm (2002 to 2005) spring SSTs.

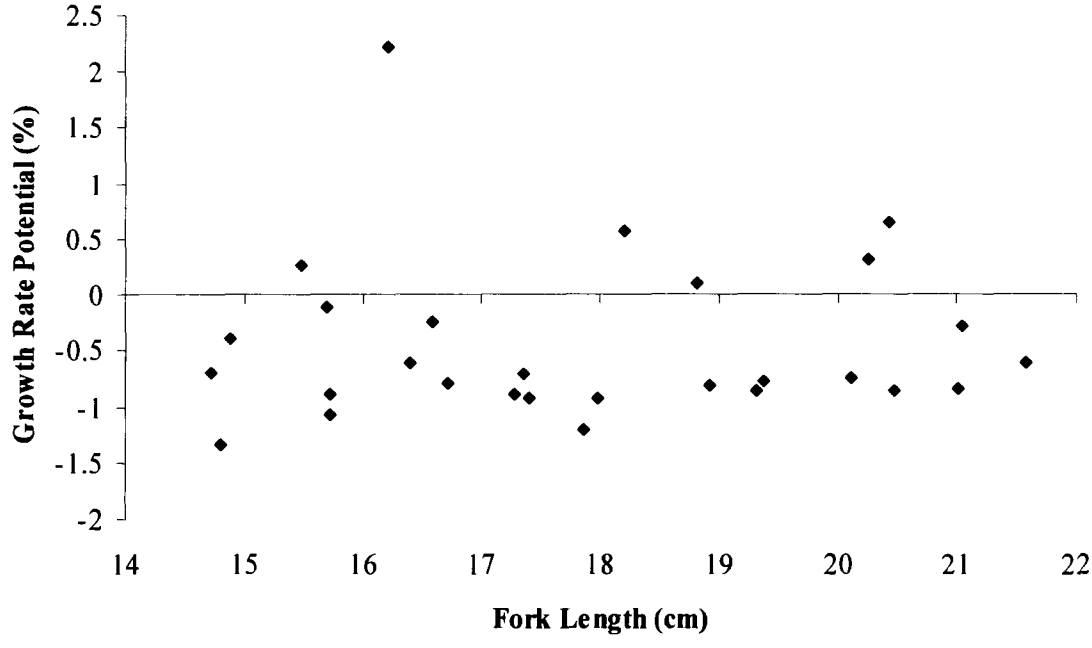

Figure 4.4. Relationship between growth rate potential (% body weight per day) and length (cm) of juvenile sockeye salmon collected during August–September 2000 to 2006 along the eastern Bering Sea shelf.

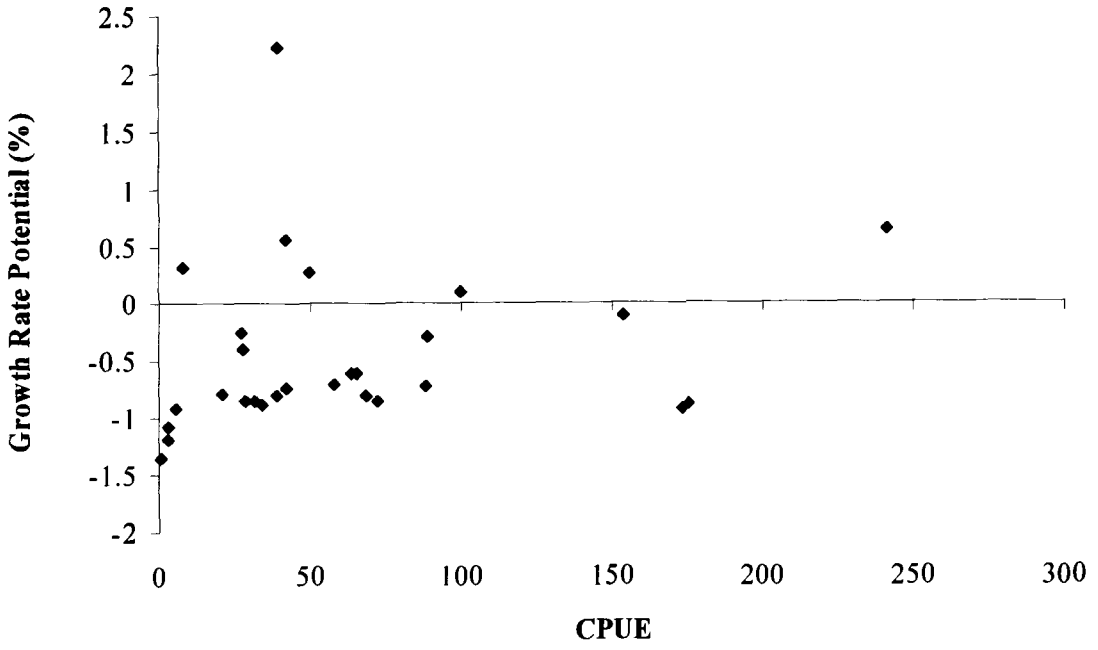

Figure 4.5. Relationship between growth rate potential (% body weight per day) and catch per unit effort (CPUE) of juvenile sockeye salmon collected during August–September 2000 to 2006 along the eastern Bering Sea shelf.

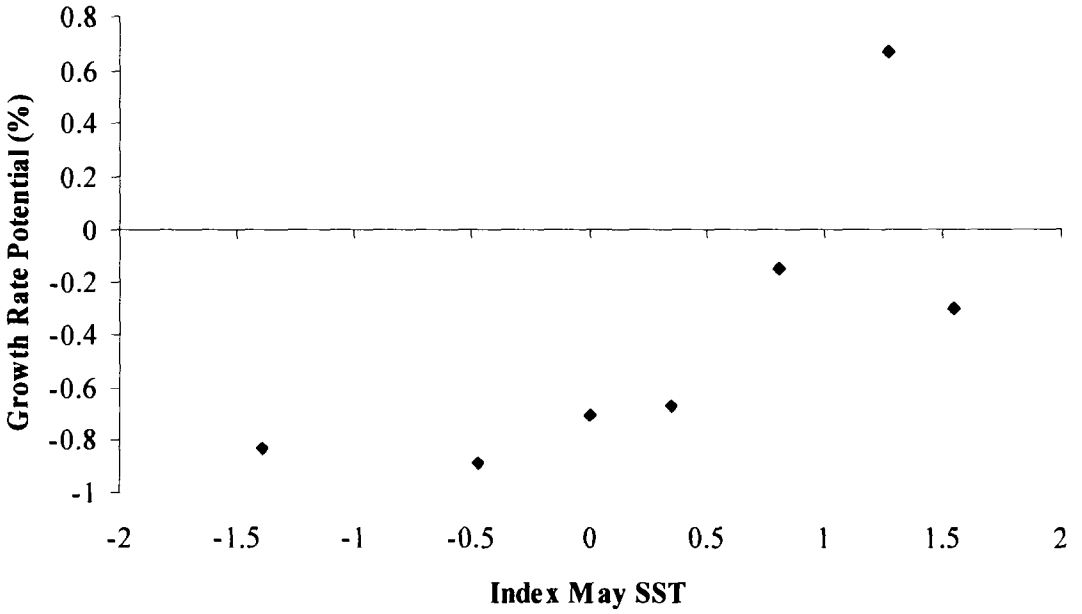

Figure 4.6. Relationship between annual averages of juvenile sockeye salmon growth rate potential (% body weight per day) collected during August–September 2000 to 2006 along the eastern Bering Sea shelf and indices of sea surface temperatures (SSTs,°C) during May 2000 to 2006.

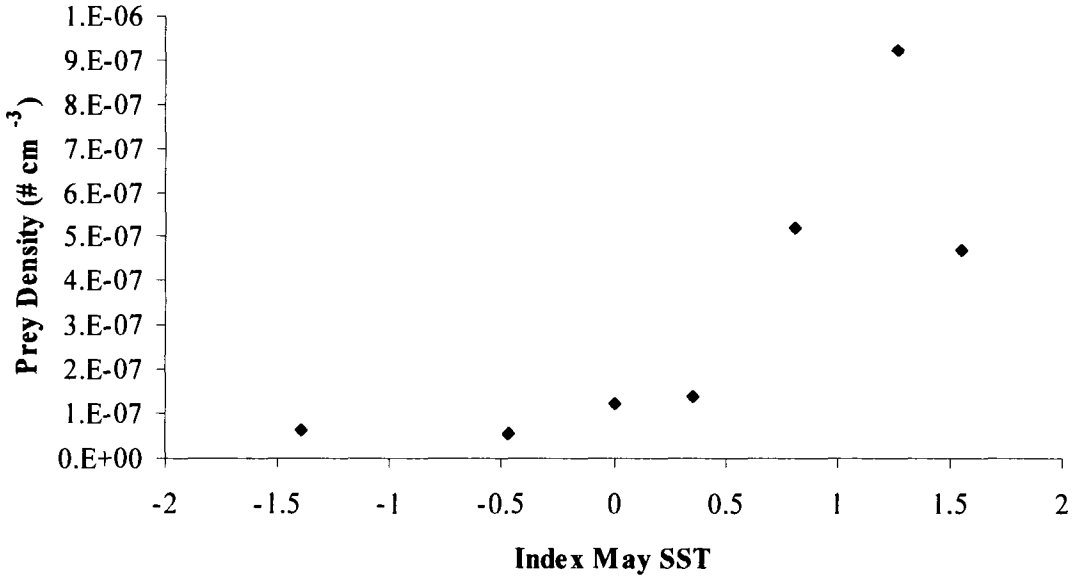

Figure 4.7. Relationship between annual averages of observed prey density (age 0 pollock and sand lance; #/cm^3) collected during August–September 2000 to 2006 along the eastern Bering Sea shelf and indices of sea surface temperatures (SSTs,°C) during May 2000 to 2006.

TABLE 4.1. Definitions of symbols used in the text. Note that subscripts *i*, *s*, and *j* represent year (*i* = 2000 to 2006), station, and region (*j* = IC, IM, OC, and OM), and overbars denote mean quantities within the definitions of *i* and *j*.

Symbol	Parameter description	Value	Source
ACT	Activity costs (cal/s)		
$\mathbf{E}$	Total energy content of juvenile sockeye salmon (cal)		
$\mathbf{ED_f}$	Caloric content of juvenile salmon (cal/g_{wet})	1,176	2
$\mathbf{ED_1}$	Caloric content of age 0 pollock (cal/g_{wet})	885	2
$\mathbf{ED_2}$	Caloric content of sand lance (cal/g_{wet})	842	2
$\mathbf{ED_p}$	Total caloric content of juvenile salmon prey (sandlance + age 0 pollock) (cal/g_{wet})	1,727	2
$\mathbf{G}$	Growth rates (cal/s)		
$\mathbf{I}$	Feeding rates (cal/s)		
$\mathbf{N}$	Number of prey caught at a station		
$\mathbf{SMR}$	Standard metabolic rates (cal/s)		
T	Sea surface temperature (°C; 5m below surface)		
$\mathbf{V}$	Volume sampled by the net (cm^3)		
$\mathbf{W}$	Sockeye salmon weight (g)		
$\mathbf{W_p}$	Prey weight (g)		
ϕ	Catchability coefficient of the net (dimensionless)	0.063	2
τ	Proportion of food that can be metabolized (dimensionless)	0.7	1
θ	Proportion of prey items captured in the net that is within the range of size range that juvenile salmon fed upon (dimensionless)		
	Consumption: $I = \frac{\rho\gamma U}{1+\rho\gamma h U}$		
ρ	Prey density (cal/cm^3)		

TABLE 4.1 continued. Definitions of symbols used in the text. Note that subscripts *i*, *s*, and *j* represent year (*i* = 2000 to 2006), station, and region (*j* = IC, IM, OC, and OM), and overbars denote mean quantities within the definitions of *i* and *j*.

Symbol	Parameter description	Value	Source
γ	Cross sectional area of the reactive field (cm^2)		
U	Swimming speed (cm/s)		
h	Handling time (s/cal)		
	Cross sectional area of the reactive field: $\gamma = \alpha_3 \cdot W^{\beta 3}$		
α_3	Intercept (cm^2)	1	1
β_3	Coefficient, γ versus W	0.69	1
	Handling time: $h = \frac{W^{(CB-1}}{ED_p \cdot CA \cdot f(T)}$		
CA	Intercept for maximum feeding rates (g/s)	0.303	3
CB	Allometric exponent of maximum feeding rate	0.275	3
$f(T)$	Temperature adjustment for maximum food consumption rates		
	Temperature adjustment function: $f(T) = K_a \cdot K_b$		
	$K_a = \frac{(0.58 \cdot L1)}{1 + 0.58 \cdot (L1 - 1)}$		3
	$L1 = \exp(G1 \cdot (T - 3))$		3
	$G1 = \frac{1}{(20-3)} \cdot \ln(\frac{0.98 \cdot (1 - 0.58)}{(0.58 \cdot 0.02)})$		3
	$K_b = \frac{(0.5 \cdot L2)}{1 + 0.5 \cdot (L2 - 1)}$		3
	$L2 = \exp(G2 \cdot (24 - T))$		3
	$G2 = \frac{1}{(24-20)} \cdot \ln(\frac{0.98 \cdot (1 - 0.5)}{(0.5 \cdot 0.02)})$		3
	Standard metabolic rates*: $SMR = \alpha_1 \cdot W^{\beta} \cdot e^{\varphi \cdot T}$		
α_1	Intercept (cal/s)	4.76×10^{-5}	4
β	Coefficient, *SMR* versus W	0.87	4

TABLE 4.1 continued. Definitions of symbols used in the text. Note that subscripts *i*, *s*, and *j* represent year (*i* = 2000 to 2006), station, and region (*j* = IC, IM, OC, and OM), and overbars denote mean quantities within the definitions of *i* and *j*.

Symbol	Parameter description	Value	Source
φ	Coefficient, *SMR* versus *T* (1/°C)	0.064	4
	Swimming costs*: $ACT = \alpha_0 \cdot W^{\delta} \cdot U^{\lambda}$		
α_0	Intercept ($cal \cdot s^{-1}$)	1.74×10^{-6}	4
δ	Coefficient, *ACT* versus *W*	0.72	4
λ	Coefficient, *ACT* versus *U*	1.6	4
	Swimming speed: $U = \omega \cdot W^{\nu} \cdot \exp^{(\kappa \cdot T)}$		
ω	Intercept (cm/s)	11.1	4
ν	Coefficient, *U* versus *W*	0.097	4
κ	Coefficient, *U* versus *T* (1/°C)	0.040	4

1. Ware (1978); 2. This study; 3. Beauchamp et al. (1989); 4. Trudel and Welch (2005)
*The oxygen consumption rates were converted from mg O_2/h to cal/s using an oxycalorific equivalent to 3.24 mg O_2/cal (Elliott and Davison 1975).

TABLE 4.2. Annual averages (±SE) of juvenile sockeye salmon growth rate potential (GRP; % body weight per day) during August – September 2000 to 2006 along the eastern Bering Sea shelf.

Year	*n*	GRP	SE
2000	35	-0.89	0.05
2001	54	-0.71	0.10
2002	80	-0.67	0.07
2003	74	-0.30	0.15
2004	44	0.67	0.27
2005	45	-0.15	0.21
2006	40	-0.83	0.06

TABLE 4.3. Regional averages (±SE) of juvenile sockeye salmon growth rate potential (GRP; % body weight per day) during August – September 2000 to 2006 along the eastern Bering Sea shelf.

Year	Region							
	IC		IM		OC		OM	
	n	GRP	*n*	GRP	*n*	GRP	*n*	GRP
2000	10	-0.89 (0.06)	4	-0.61 (0.13)	11	-1.07 (0.04)	10	-0.81 (0.15)
2001	12	-0.40 (0.44)	13	-0.70 (0.11)	2	-0.78 (0.06)	27	-0.85 (0.02)
2002	19	-0.80 (0.10)	14	-0.25 (0.27)	26	-0.84 (0.07)	21	-0.61 (0.17)
2003	3	-1.34 (0.07)	23	0.11 (0.41)	8	-1.20 (0.04)	40	-0.28 (0.14)
2004	9	0.27 (0.62)	7	2.22 (0.63)	11	0.56 (0.64)	17	0.31 (0.31)
2005	10	-0.89 (0.24)	7	-0.11 (0.42)	11	-0.72 (0.35)	17	0.64 (0.39)
2006	12	-0.85 (0.11)	4	-0.92 (0.16)	8	-0.92 (0.08)	16	-0.74 (0.10)

TABLE 4.4. Sensitivity of bioenergetic model estimates of juvenile sockeye salmon growth to 20% perturbations in the annual observations of SST (°C) and prey density (number/cm^3) at each station during the August to September (2000 to 2006) BASIS surveys of the eastern Bering Sea shelf. A value of 1.0 means that a 20% increase in a value of SST or prey density from its nominal value caused a 20% increase in growth rate potential.

	Temperature (°C)		Prey Density (number cm^{-3})	
Year	-20%	+20%	-20%	+20%
2000	0.6	-0.7	-0.2	0.2
2001	0.6	-0.7	-0.3	0.3
2002	0.8	-0.9	-0.5	0.5
2003	1.7	-2.2	-2.0	1.7
2004	0.1	-0.3	-1.7	1.4
2005	3.5	-4.8	-5.4	4.8
2006	0.6	-0.7	-0.2	0.2

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